RADIOGRAPHIC ANATOMY AND DEVELOPMENT
OF THE CETACEAN FLIPPER

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I. INTRODUCTION

A. Introductory Remarks

Much of current knowledge about bone structure, mechanics, development, physiology, and pathology has been learned from research using small animal models; rats, rabbits, and chickens have been especially popular. While small animal studies have been extremely valuable, the applicability of conclusions from small animal models to human bone is always uncertain, as is the case with all animal models of human systems.

Ideally the choice of a particular species as a model for human systems should be based upon a specific set of characteristics which render that animal particularly suited for comparison with homologous human systems. This concept, or the August Krogh Principle ("For many problems there is an animal on which it can be most conveniently studied"), was first clearly expressed by Krogh in 1929 and later elegantly elaborated by Sir Hans Krebs (1975). Among other points, Krebs stressed that the advantages of large physical size and convenient anatomic arrangement should be considered in the selection of a good experimental material with which to tackle a biological problem. More often than not, animal models are selected for reasons of general laboratory convenience, expense, previous experience, and availability. While these are valid considerations, it is important to remember that there is little reason why rats, rabbits, and chickens should be the only animal models of human bone.

Indeed, small animals such as the mouse and rat differ significantly from humans in several respects: a) very little, if any, Haversian bone is found in these animals, b) epiphyseal calcification and ossification take place without the antecedent vascularization by cartilage canal systems which occurs in man (Becks, et al, 1948) and c) cessation of growth in the rat does not always occur with epiphyseal union with the metaphysis so that the growth plate may remain cartilaginous throughout adult life (i.e., the "lapsed union", Ogden, 1977). In short, human bone development and growth involves mechanisms which may be absent in small animals.

It is well known that the gross proportions and forms of bone are different in larger animals from those in smaller animals (Thompson 1961, McMahon 1973). Yet the question of whether large animals have identical, different, or additional mechanisms of bone development and growth is virtually unexplored. Is there a critical size for a bone at which a secondary ossification center becomes a normal mechanism of growth? Is there a critical bone or species size at which the ossification of an epiphyseal center requires cartilage canals and vascularization of the chondreoepiphysis? Is the rate or onset of epiphyseal or primary center ossification related to the form or function of the bone? The answers to these and many other questions must await studies of normal and abnormal bone development and growth in large animals.

B. Previous Studies

Anatomy. The gross anatomy of the cetacean pectoral limb or flipper[1] is well described (Flower 1876, Howell 1930a, Felts 1966). The flipper has undergone great modification from its presumed terrestrial mammalian ancestor to its present form. Externally (figure 1) it is a smooth surfaced streamlined fin-shaped paddle well adapted in form to its function as a biological hydroplane roughly analogous to the ailerons of an airplane. Unlike the forelimbs of the Pinnepedia or seals, the whale flipper apparently plays only a very small role in providing propulsive force; instead, its primary role is to control the attitude and direction of the animal in the water, and to steer the animal as it swims (Howell 1930a). In addition the flipper serves as an organ of heat exchange or heat conservation (Scholander and Schevill, 1955) and can be used to manipulate objects as observed in cetaceans in captivity (Brown 1960, Kritzler 1952). The limb does not bear weight in the terrestial sense, but it is subjected to loading by water resistance and body inertia, especially when the flipper is altered from the neutral or glide position.

The internal or bony architecture of the cetacean flipper (figure 2) retains some degree of homology to that of terrestial animals, but several features are immediately apparent on even the most casual inspection. The proportions of the cetacean flipper are altered so that the elbow is at approximately the axilla of the animal and virtually

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[1]As distinguished from the dorsal fin or the caudal flukes.

the entire visible extremity is composed of antebrachium and manus. The number of phalanges per digit can be many more than the terrestial mammalian complement of three, a condition known as hyperphalangy. None of the bones show any evidence of a medullary canal. Flippers from older animals often show bony fusions of varying joints, most often at the elbow and the carpus.

Osteology

The cetacean humerus is a short, sturdy, essentially cylindrical bone with a proximal humeral head which articulates in a synovial joint with the scapula, and articulates distally end-on with the radius and ulna in a rigid elbow joint. The radius and ulna are both flattened and somewhat wedge-shaped in cross-section, so that the two side by side give a streamlined cross-section to the flipper. The carpal bones vary in number and position from species to species, individual to individual, and often from right to left in the same individual. In the odontocetes or toothed whales the carpals usually number five or six, typically with a proximal row of three and a distal row of two or three. In the mysticetes or baleen whales the carpus is reported to have as many as nine (in Eubalena) or as few as three (in Balena) (Howell 1930a). There is a single mention (Flower 1876) of secondary ossification centers in the carpal bones of Physeter: this is particularly significant since carpal secondary centers are otherwise not known to occur in any animal.

There are five digits in the odontocetes and a few mysticetes, but most mysticetes have four. Which digit is the "missing" digit has been the subject of controversy (e.g., Kukenthal 1890b). The pollex

and the fifth digit are short, the latter especially variable with
flipper shape so that it is very short in the long narrow flipper of
Globicephala and longer in the broad flipper of Eubalena (figure 2).
The second and third digits are always the longest, with the second of-
ten longer than the third. The metacarpals are considered indistin-
guishable from the phalanges in their form and function (or lack there-
of). The metacarpals and the phalanges develop epiphyseal ossification
centers at not one, but at both ends of each bone.

Hyperphalangy of the digits is a characteristic unique among
mammals to the cetaceans, and is most marked in the longest, i.e.,
the second and third digits. The number of phalanges per digit, like
the configuration of the cetacean carpus, varies with the species, the
individual, and with the flipper. The phalangeal formula is also quite
variable with author, e.g.:

	(Felts 1966)						(Ridgeway 1972)				
	I	II	III	IV	V		I	II	III	IV	V
D. leucas	3	8	6	5	4		1-2	6 - 7	4 - 5	2-4	2-4
T. truncatus	1	7	5	2	1		2	9	7	4	2
G. melena	4	15	11	3	2		3-4	9-14	9-11	2-3	1-2

Hyperphalangy, its phylogeny and its ontogeny have been the subjects
of much speculation. In 1930 Howell reviewed the published theories;
additional speculation, but little knowledge has been added since then.

The bones of the cetacean flipper are continuous, spongy, can-
cellous bone without a well-defined cortex, or any medullary cavity or
marrow space. The amedullary character of cetacean bone is shared by
two other secondarily marine forms, the manatee (Fawcett 1942) and the
penguin (Meister 1962). Both manatee bone and penguin bone have much
higher overall densities (i.e., dry bone weight/whole bone volume) than

that of cetacean bone, which is comparable to that of human bone (Felts and Spurell 1965). Meister has reviewed the theory that in the adaptation of terrestial forms to marine life, dense amedullary "pachyostotic" bone evolved as an adaptation useful for overcoming buoyancy, and that later forms, presumably including cetaceans, developed more rarified spongy amedullary "post-pachyostotic" bone. Fawcett proposed an alternate hypothesis that the manatee, whose thyroid histology is consistent with hypothyroidism, and whose resting oxygen consumption is very low compared to other marine mammals, shows slow ossification and suppressed resorption comparable to that seen in clinical hypothyroidism. Whether or not this theory is applicable to cetaceans is unclear.

Arthrology

It is generally agreed that in the cetacean flipper, all joints distal to the shoulder are essentially immovable and that this is a functionally advantageous adaptation. However, precisely what kind of joints do or do not exist is uncertain. Struthers (1871) reported finding apparently partial synovial joints across the middle of some of the larger interphalangeal joints of an adolescent fin whale[2]. Flower (1876) wrote that in odontocetes the phalanges are often connected by "imperfect synovial joints", and that mysticetes always have fibrous joints except for the cartilages containing the carpals and the phalanges which are "confluent" (i.e., synchondroses?). Howell (1930a), and Harrison and King (1965) state that all joints except the shoulder are fibrous joints, while Felts (1966) and Felts and Spurell (1965, 1966) call the elbow a synchondrosis and leave unclear the type of joint between the carpals and the phalanges. Many authors have commented on the existence

[2] a mysticete

of joint ankyloses in older animals, but they otherwise remain unin-
vestigated.

Myology

Except for some early reports of rudimentary digital flexors
and extensors in the finwhale (Struthers 1871, 1889), narwhale (Howell
1930b), the Greenland Right whale (Struthers 1877), and Hyperodon bidens
(Struthers 1873), there is no musculature in the cetacean flipper dis-
tal to the shoulder complex. Instead of muscles, the skeletal elements
of the flipper are reinforced by numerous strong dorsal and ventral
ligamentous bands, connecting the humerus, the forearm bones, the car-
pals, and the digital bones into a single unit with only very limited
passive flexibility.

Vasculature

The vascular supply of the whale flipper has been studied in
Laegenorhychus acutus and Tursiops truncatus and was found to consist
of 1) centrally located arteries, each surrounded by several thin-
walled veins forming a 2) circumarterial venous conduit, supplemented
by 3) thicker-walled simple veins located superficially and forming a
plexus beneath the dermis. The authors proposed that the circumarterial
venous system and the artery form a countercurrent vascular heat ex-
change system which would allow for maximum heat conservation, while
the superficial venous system would allow for an alternate flow pattern
to facilitate heat loss through the flipper when needed. (Scholander
and Schevill 1955).

Pathology

The only report of bone pathology in a cetacean I have encoun-
tered is that of Cowan (1966) who examined bones collected from "grave-
yard beaches" where flensed carcasses were washed ashore and decomposed
after processing by a commercial whaling station. Cowan found anomalies
of the vertebrae, such as asymmetry of the transverse processes, arch
closure defects (i.e., spina bifida), and "congenital block vertebrae"
(i.e., fusion at the lateral margins of the vertebral bodies) to be
the most common abnormalities. He also reported cases of healed rib
fractures, and a case of "severe extensive osteoarthritis and fusion
of several vertebrae", "comparable with degenerative disc disease in
humans".

Flipper Development and Growth

Only a few authors have published work on the patterns of devel-
opment and growth of the cetacean flipper. The nineteenth and early
twentieth century investigators (Ryder 1885a,b, Kükenthal 1888a,b,
1890a,b, Kunze 1912, and Leboucq 1889) who studied pre- and postnatal
specimens were concerned primarily with the problems of hyperphalangy
and carpal anatomy, and commented little on questions about flipper de-
velopment and growth. Kükenthal (1888a) did note that the cartilaginous
carpals underwent fusion to one another in varying combinations during
pre- and postnatal development and growth. In the same paper, Kükenthal
proposed that the number of phalanges per digit decreased with increasing
age. Kunze agreed with this "law" of Phalangenreduktion, while Weber
(1888) wrote that the number of phalanges increases with age. Seventy-
five years later, Felts (1966) granted that the phalanges "may vary with
time" but did not specify further.

The most detailed articles yet published on the growth and development of the cetacean flipper have come from Felts (1966) and from Felts and Spurell (1965, 1966). According to these studies, the primary ossification centers appear in a proximal to distal sequence. The sequence of appearance of the secondary centers in D. leucas and Globicephala melena is reported by Felts (1966) as proximal humerus, then distal humerus, proximal radius and ulna, and finally distal radius and ulna. The sequence of epiphyseal fusions is given as distal humerus, proximal radius and ulna, proximal humerus (occuring at age approximately one year for Globicephala), then distal radius and ulna; the latter remain incompletely fused even in old animals (Felts and Spurell 1966). Felts does not comment on the ossification of the carpals other than that they are "erratic", but does note that the digits show a "striking slowness of ossification". He writes that phalangeal bony epiphyses are found only in the "very largest" Globicephala, in an old male specimen of T. truncatus, and not at all in D. leucas, even when all other epiphyses in the flipper are fused (Felts 1966).

Even fewer studies have attempted to study quantitatively the development and growth of the flipper. Studies of growth and development of the whale are greatly complicated by the fact that both longitudinal studies and population studies are performed only with difficulty. Raising whales and dolphins in captivity for serial observations is obviously beyond the capabilites of almost all prospective investigators. Population studies are best performed with large numbers of animals or specimens, but the supply of cetaceans available for study is very limited. In addition, the determination of the age of an individual cetacean is an approximation at best. The examination of annual dentin layers in teeth

is the method most widely used in odontocetes (Sergeant 1959, 1962a, Hui 1977). The method is obviously inapplicable to mysticetes, which have no teeth. At all ages, the examination of dentin layers is subject to significant observer variation, and beyond approximately ten or twelve years of age the method becomes increasingly unreliable.

Sergeant (1962b) compared flipper size relative to body length in the four species of genus Globicephala by measuring flipper length and body length in 57 G. melena and using data previously reported by other authors for G. melena edwardii, G. scammoni, and G. macrorhyncha. His study showed that G. melena and the subspecies G. m. edwardii had the proportionately longest flippers of the four species, and that these flippers grow more rapidly in length than does the body, (i.e., the flipper length/body length ratio increases) throughout all but earliest postnatal life; while the growth of G. macro flippers[3] remains proportionate to growth in overall body length, so that the ratio of flipper length to body length remains relatively constant at approximately 16%. G. scammoni was intermediate in both rate of growth and in proportional flipper length.

Omura et. al. have published a series of papers (1970, 1971a, 1971b, 1972) reporting the measurements of the sizes of skeletal bones, including the flipper bones, of several odontocetes and mysticetes, but they have made no reported attempt to relate these data to patterns of growth, either in the animal or in the flipper.

In an attempt to define an easily observable index of physical maturity which would also correlate with sexual maturity, Hui (1975) proposed a "flipper index" which was obtained by scoring the degree of

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[3]It should be noted that Sergeant based his conclusion on data on only four flippers, from four authors.

epiphyseal fusion of the radius, ulna, metacarpals, and phalanges, and

adding these scores for both flippers together to obtain the flipper

index for that animal. Unfortunately, the exact criteria and methods

of scoring were not explained. In Delphinus delphis, Hui found that the

flipper index was correlated reasonably well with the testis weight in

males and could provide a fairly reliable estimate of testes develop-

ment and sexual maturity. In comparison both animal length and den-

tin ages showed a much poorer correlation with testis weight, and testi-

cular development and sexual maturity could not be estimated with any

confidence at all over a wide range of values. Unlike in males, the

flipper index in females was shown to be a poor measure to indicate

ovarian scars and hence prior ovulation and sexual maturity. Again,

dentin layers and animal length were not evidently related to sexual

maturity.

The only reports of the histology of bone development in the

cetacean flipper are those of Felts, who briefly described the develop-

ment of the humerus (Felts and Spurell 1965) and the radius (Felts and

Spurell 1966) in embryonic and fetal specimens of D. leucas, B. physalus

and G. melena:

> The cavity of the shoulder joint is evident in the youngest
> specimen . . . but the elbow joint is united by fibrous tis-
> sue from the earliest stages[4]. The gradient of cartilage
> maturation from middle toward either end is not as distinct
> or as organized as in common land mammals. In particular,
> the zone of flattened cells indicative of rapid longitudinal
> growth (Streeter 1949) is absent. In addition, at no time in
> embryonic and early fetal periods are there regular rows of
> hypertrophic cells in the central region or adjacent to the
> advance of ossification.(Felts and Spurell 1966).

Felts also reports in the same paper that the extent of pre-osseous cal-

cification of cartilage and the lag-time until the subsequent replacement

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[4] Does Felts mean to imply that the elbow starts out as a syndesmosis
and then later changes into a synchondrosis, as he elsewhere calls
the elbow?

by osseous tissue are both much greater than in previously studied bone.
The pattern of endochondral ossification within the developing bone is
more irregular and does not form a regular front of ossification, but
rather a pattern of calcified cartilage remnants lying between irregular
invasions of primitive vascular tissue. And as mentioned before, re-
modeling and reorganization of the trabeculae apparently take place only
very slowly, without any net resorption to form a medullary cavity.

Neither the histology of the cetacean epiphysis and growth plate,
nor the histologic development, maturation, and fusion of the cetacean
epiphyseal ossification center have ever been described.

Felts and Spurell (1965, 1966) studied the internal structural or-
ganization and density in both the humerus and the radius by photoden-
sitometry of radiographs of sawed bone sections, and by direct weight
and volume measurements of excised bone sample. He found that both bones
showed "endoectad gradients of porosity" so that in the humerus, bone
was most dense on the dorsal and ventral sides, less dense on the anterior
and posterior sides, and least dense in the core, with a discernable
trabecular orientation along trajectories consistent with the stresses
of the flipper. More importantly, in his study on cetacean radii, he
demonstrated an hourglass-like distribution of less dense bone within
the radii of the beluga, the finback and pilot whale (figure 3). This
hourglass of less dense bone almost certainly represents cones of endo-
chondral bone surrounded by the denser perichondral bone[5]. In the beluga
whale, the author was even able to demonstrate a radiographically visible
outline of the neonatal radius within the adult bone (figure 3). In this
paper, Felts and Spurell (1966) used the cones as the basis of a simple
model for the growth of the radius.

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[5]Similar cones of endochondral bone can be seen in the human fetal femur.
  (Gardner and Gray 1970).

C. Why Study the Cetacean Flipper?

Given the relative lack of resorption and remodelling, and the ease of distinguishing endochondral bone from periosteal bone, the cetacean flipper seems to offer an animal model well suited to the study of the geometry of bone growth, and especially to the study of the spatial and temporal relationships of the contributions of periosteal and endochondral bone formation to the structure of the mature bone. Unlike the typical terrestial mammalian bone, in which comparatively extensive resorption and remodelling erases all but the most immediate history of bone development and growth, the bone of the cetacean flipper retains its developmental history to an extent unmatched by that of any other mammal.

This unique attribute of the cetacean flipper would be reason enough to justify its study. But in addition, the adaptation of the cetaceans to a purely aquatic environment and consequent changes in limb function; the effects that size and scale must have on the structure of bone as a tissue and on each bone as a structural unit in this, the largest of all animals; and the relative lack of knowledge on the development and growth of bone in large mammals all justify the study of the mighty whale.

As we have seen, some of the fundamental descriptive anatomy of the flipper and much of the basic knowledge of patterns of growth and development of the flipper remains uncertain. Precisely what kind of joints are in the flipper? Does the number of phalanges change with age or growth? Is there any consistent pattern to the variations in carpal

anatomy and phalangeal numbers between species? Between individuals?
Can the physical maturity of the flipper be described quantitatively
and related to the sexual and overall physical maturity of the animal?
Are there carpal secondary centers?

This study cannot and does not attempt to investigate all of
the questions above, especially in view of the limits of available
materials and time. I will attempt to clarify the nature of the joints
of the flipper, the presence or absence of secondary centers in the
carpus, and the radiographic patterns of growth and development in
the flipper, including changes (if any) in the phalangeal counts, in
a fairly complete postnatal series of flippers from Globicephala macro-
rhyncha.

II. MATERIALS AND METHODS

One hundred flippers from twenty-nine male and sixty-nine fe-
male individuals identified as Globicephala macrorhyncha[6] were kindly
provided by Dr. James G. Mead of the Division of Mammals, Museum of
Natural History of the Smithsonian Institution. These specimens were
collected by JGM and his associates from several herd strandings which
had taken place over the past two years. The flippers had been disarti-
culated in the field at the shoulder joint and were supplied to us in the
frozen, unfixed state. Data on body lengths for all animals and body
weights for twelve males and twenty-two females were also provided.
These data are given in tables 1 and 2.

In addition, Dr. Mead generously made available for our use radio-
graphs of flippers from a series of fifteen male and thirty-six female
G. macrorhyncha not represented in the collection of specimens provided
to us. Throughout the rest of this study, this series of radiographs will
be conveniently referred to as the "Smithsonian series" to distinguish
it from the series of flipper specimens which will be referred to as the
"Yale series". For the Smithsonian series, data was also available for
the majority of animals on body length; the presence or absence of thor-
acic vertebral epiphyses (as an indicator of overall physical maturity);

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[6]Globicephala macrorhyncha, also known as the short-finned or tropical
pilot whale or blackfish, is a small odontocete found in the tropical
Atlantic or Indian Oceans. It is distinguished from its close relative
the North Atlantic pilot whale G. melena by a shorter flipper and some
cranial characters. Body length at birth is approximately 180-190 cm.
for both sexes. Females grow to about 450 cm. while males may reach
600 cm. (Sergeant, 1962a).

TABLE 1

MALE G. MACRORHYNCHA FLIPPERS -- YALE SERIES

Specimen Number	Flipper Length (cm)	Animal Length (cm)	Animal Weight (kg)
C - 28	90.0	507	-
C - 39	79.0	417	920
C - 40	61.5	358	-
C - 42	69.0	384	660
C - 46	75.0	425	-
C - 59	56.0	304	-
C - 104	42.5	262	-
C - 108	70.0	373	-
C - 119	65.5	347	-
C - 120	89.5	510	1460
C - 125	67.5	360	-
C - 126	61.5	351	500
C - 129	59.0	308	-
C - 131	48.0	280	280
C - 132	41.0	227	160
C - 135	84.5	427	-
C - 136	80.0	479	1390
C - 137	69.5	403	830
C - 152	85.0	450	-
C - 153	59.0	313	-
C - 157	64.0	380	-
C - 160	73.0	360	-
C - 183	49.5	268	270
C - 186	37.0	223	180
C - 189	50.5	289	300
C - 192	79.0	381	-
C - 199	89.0	470	1300
C - 204	61.0	324	-
C - 223	86.0	468	-

TABLE 2

FEMALE C. MACRORHYNCHA FLIPPERS - YALE SERIES

Specimen Number	Flipper Length (cm)	Animal Length (cm)	Animal Weight (kg)
C - 12	65.0	378	-
C - 27	72.0	382	-
C - 37	59.0	326	430
C - 38	58.0	365	-
C - 41	65.5	367	630
C - 45	62.0	354	550
C - 47	69.0	380	-
C - 48	60.5	328	510
C - 60	66.0	328	-
C - 61	62.5	337	-
C - 62	60.0	340	-
C - 63	66.0	317	-
C - 69	64.5	369	-
C - 89	65.0	346	-
C - 90	66.0	375	720
C - 91	35.0	209	-
C - 92	63.0	356	-
C - 93	38.0	226	-
C - 102	57.0	350	590
C - 103	58.0	332	-
C - 105	59.0	357	670
C - 106	66.5	380	-
C - 110	66.0	385	960
C - 111	60.5	356	-
C - 112	61.0	342	-
C - 113	58.0	350	-

Table 2 continued from page A.

Specimen Number	Flipper Length (cm)	Animal Length (cm)	Animal Weight (kg)
C - 114	53.5	301	-
C - 116	64.0	360	-
C - 118	64.0	361	-
C - 121	64.0	366	-
C - 122	56.5	339	-
C - 123	63.0	347	650
C - 124	54.0	285	-
C - 127	46.5	277	-
C - 128	60.0	351	460
C - 130	58.5	346	550
C - 133	57.0	321	600
C 0 134	67.0	369	710
C - 138	62.5	365	700
C - 139	58.0	334	-
C - 140	60.5	349	-
C - 142	63.0	370	630
C - 144	56.0	343	-
C - 145	59.0	348	-
C - 147	62.0	375	-
C - 148	62.0	349	560
C - 150	59.0	360	620
C - 154	60.0	351	-
C - 155	58.5	346	-
C - 156	58.0	327	-
C - 158	66.0	388	-
C - 159	63.0	363	-
C - 161	50.5	301	-
C - 162	54.0	328	-
C - 163	41.0	253	-
C - 164	63.0	360	-

Table 2 continued from page B.

Specimen Number	Flipper Length (cm)	Animal Length (cm)	Animal Weight (kg)
C - 165	60.0	379	-
C - 166	66.0	378	-
C - 167	62.5	369	-
C - 168	58.5	368	-
C - 183	66.5	381	720
C - 184	58.5	327	360
C - 185	55.5	325	540
C - 187	67.0	370	660
C - 188	60.5	367	630
C - 194	59.5	342	-
C - 201	45.0	257	-
C - 202	61.0	357	-
C - 224	55.5	328	-

testis weights for the males, uterine size, number of ovarian scars, and presence or absence of pregnancy and lactation in females (as indicators of sexual maturity). These data are summarized in tables 3 and 4.

Unfortunately, except for radiographs from a single male fetus in the Smithsonian series, no prenatal specimens or radiographs were available for this study. Both males and females were represented at all stages of post-natal development, with the possible exception of a lack of old males.

The age and size distributions of both series of flippers and radiographs must be considered biased in that they reflect the composition of the herds from which these samples were gathered. The herd structure of the closely related G. melena (Sergeant, 1962) comprises predominately females of all ages and a smaller number of mostly immature and adolescent males with few mature males. The adult males apparently segregate and form separate small herds. In addition, the death rate at all ages is higher for males, so that while equal number of males and females are born, males comprise only about one-quarter of the population of animals older than about fifteen years. The male samples used in this study are predominately adolescent animals, and the bulk of the females in these samples are mature animals.

Most of the animals in the Yale series were represented by a right flipper only or a left flipper only; most of the animals in the Smithsonian series were represented by radiographs of both flippers. The assumption of bilateral symmetry of flipper length, number of phalanges, number of and stage of ossification centers was tested using two-tailed T-tests for paired comparisons. No significant differences between right and left

TABLE 3

MALE G. MACRORHYNCHA FLIPPER RADIOGRAPHS

SMITHSONIAN SERIES

Specimen Number	Flipper Length (cm)	Animal Length (cm)	Thoracic Vertebral Epiphysis	Testes Weight (gram)
500200	93	535	Fused	1580
500206	44	253	-	20
500207	91	488	Open	980
500208	86	481	Open	600
500209	75	411	Open	190
500211	67	371	Open	100
500215	71	392	Open	200
500219	32	183	Open	-
500220	67	363	Open	800
500225	70	358	Open	800
500231*	25	142	Open	-
500233	84	525	Fused	-
500235	73	405	-	130
500236	85	476	Open	-
500240	85	481	Open	600

*fetus

TABLE 4

FEMALE G. MACRORHYNCHA FLIPPER RADIOGRAPHS

SMITHSONIAN SERIES

Specimen Number	Flipper Length (cm)	Animal Length (cm)	Thoracic Vertebral Epiphysis	Sexual Maturity
500196	70	386	Fused	Yes
500197	56	325	Open	No
500198	58	336	Open	No
500199	58	343	Open	Yes
500201	66	392	-	-
500202	57	351	Closed	Yes
500203	65	378	Fused	No
500204	61	384	Fused	No
500205	54	305	Open	No
500210	66	385	Fused	Yes
500212	60	359	Open	No
500213	62	397	-	-
500214	55	355	Open	Yes
500216	59	340	Open	Yes
500217	70	384	Fused	Yes
500218	34	195	-	-
500221	53	307	Open	Yes
500223	65	378	Fused	Yes
500224	69	389	Fused	Yes
500226	59	326	Open	Yes
500228	54	320	Open	Yes?
500229	58	368	Fused	Yes
500230	58	366	Fused	Yes?
500231	57	363	Open	Yes

Table 4 continued from previous page.

Specimen Number	Flipper Length (cm)	Animal Length (cm)	Thoracic Vertebral Epiphysis	Sexual Maturity
500232	66	377	Open	No
500234	52	293	Open	Yes
500237	53	358	Open	Yes?
500238	59	378	Open	Yes?
500239	55	383	Fused	Yes?
500241	60	366	Open	Yes?
500242	66	375	Fused	Yes?
500243	53	331	Open	No
500244	58	376	Closed	Yes?
500245	38	236	Open	No
500242	59	376	Open	Yes?

flippers were revealed at the P<0.05 level of confidence. Therefore, for the studies in this report, redundant right flippers in females and redundant left flippers in males were arbitrarily excluded in order to avoid the bias of data duplication from animals which happened to have both flippers represented in the sample.

All flippers received by us were entered into the specimen log and radiographed. Standard views included where practicable; a dorsal-ventral view of the entire flipper using radiographic film in cassettes; dorsal-ventral detail views of the proximal half of the flipper to include the humerus, radius, ulna, and carpus, using industrial film without cassettes; and an antero-postero view of the humerus.

The radiographs were read and scored using a standard form (figure 4). The species, sex, animal length and animal weight were entered as given by the Smithsonian Institution. Flipper lengths were taken from measurements from the radiographs of the direct distance from the most proximal aspect of the humerus (either the humeral head or the tubercle) to the distal tip of the flipper, to the nearest 0.5 cm. It should be noted that this method of measurement is not a standard measure of flipper length (Norris 1961). However, a t-test for paired comparisons on a sample of flippers was performed and did not show a significant difference between this measurement and the standard measurement of straight-line length from the anterior insertion of the flipper into the body contour at the $P < .05$ level of confidence. The more easily performed x-ray measurement was used throughout this study.

The number of primary ossification centers was noted for each digit and for the carpus. The absence or degree of development of each

epiphyseal ossification center was scored using the following criteria:

Absent: no radiographic evidence of an epiphyseal center.

Appearing: evidence of a bony epiphyseal center with a width
              of less than one-fourth that of the metaphsyis.

Developing: a bony center between one-fourth and three-fourths
              the width of the metaphysis.

Open: a mature bony epiphysis without evidence of clos-
              ure of the physis.

Joined: a mature bony epiphysis with loss of the radiolucent
              physeal line over less than one-half of the width
              of the physeal region.

Closed: a mature bony epiphysis joined to the metaphysis
              over the greater than one-half of its width.

Fused: a mature bony epiphysis joined to the metaphysis
              with little or no evidence of a previous physis.

It should be noted that while these are primarily objective criteria, there was of necessity considerable subjective interpretation in the reading of each radiograph, given the practical impossibility of obtaining a perfect view of each epiphysis of each flipper.

After all radiographs had been read, and a pattern of epiphyseal development and fusion had emerged as a normal sequence, each flipper was rated on an arbitrary scale of radio-ulnar maturity (see Observations and Data section).

Photography and limited dissections of specimens were carried out on a series of flippers representing various stages of maturity. A limited number of flippers were grossly sectioned. The proximal half of the humerus was removed with a transverse saw cut through the flipper and sectioned vertically along its long axis in order to examine the proximal humeral ossification centers. The remainder of the flipper was sectioned horizontally through the plane of the flipper.

Selected specimens were fixed in 10% formalin and submitted for histologic preparation for microscopic studies. Unfortunately, because of time constraints neither celloidin nor paraffin sections were ready for examination at the time of this report.

Selected flippers were submitted to the Peabody Museum of Natural History for processing by Dermestid larvae, which consume the soft tissues but leave the bones intact. Unfortunately, in so doing the larvae also destroy the cartilage and ligaments so that the relationships between bones is also destroyed.

Data plotting and analysis were carried out at the Yale Computer Center.

III. OBSERVATIONS AND DATA

In this section, the gross anatomy of the flipper of G. macro-
rhyncha will be briefly discussed, and observations on the patterns of
development and growth from both the radiographic study and gross speci-
mens will be presented.

A. Gross Anatomy

Globicephala macrorhyncha and the others of its genus have a par-
ticularly long and narrow flipper, with uniform black color over its sur-
face. The unfixed flipper is a virtually rigid unit, with no movable
joints and only a very limited dorso-ventral flexibility at the distal
end.

The epidermis of the flipper is relatively thick and has a waxy
consistency. The dermis is very tightly adherent to and merges with the
dense fibro-fatty hypodermis, which in turn was indistinguishable from
the dense connective tissue which filled in the outline of the flipper
and the interdigital spaces. The amount and character of the subcutan-
eous fibro-fatty tissue varied from two to three cm. thick and quite fat-
ty proximally near the flipper-body junction, to more fibrous and very
thin on the dorsal and ventral surfaces of the distal flipper, so that the
phalanges distally lay almost immediately subcutaneously.

In the flippers of G. macrorhyncha only the muscles of the should-
er girdle were found, inserting as far distal as the mid-humerus. No at-
tempt was made to dissect and identify the individual muscles. No muscles
were found distal to these. A tough, thick layer of fibrous periosteum
invested the non-articular surfaces of the humerus, radius, and ulna,

with ligamentous thickenings connecting these bones to one another. The carpals, metacarpals, and phalanges were covered with a similar but thinner layer, which became even thinner as one proceeded distally. The ligaments which coursed down the digits occupied a position analogous to that of digital flexors and extensors, with the exception that these ligaments often crossed from one digit to another, especially between the second and third digits over the metacarpals and proximal phalanges.

A small axillary artery was noted, as were superficial plexuses of thin-walled veins on both the dorsal and ventral surfaces of the flipper. No other large vessels were encountered during these limited dissections.

3. Patterns of Growth and Development

Bone Structure. The endochondral cones of less dense bone re-
ported by Felts could be seen in the humerus, radius, ulna, metacarpals,
and in the proximal phalanges of G. macrorhyncha on close inspection
of the sectioned specimens. Unfortunately, these endochondral cones are
not well revealed by the photographs. They are perhaps best seen in
figure 7. The cones are faintly visible in most of the radiographs and
quite clearly visible in some radiographs, especially those of younger
flippers (figure 5). It is difficult to say whether this difference in
visibility is an artifact of the larger amount of obscuring soft tissue
in the larger animals or whether there actually exists a more marked dif-
ference in the bone density in the younger animal.

Flipper Size

Graph 1 shows a linear relationship between flipper length and
animal length in males. An ordinary least squares regression of flipper
length on animal length yielded a Pearson r-coefficient of $r = .980$, a
slope $= 0.181 \pm 0.0014$ (SE), and a t-statistic of 128 for 41 animals;
i.e., a highly significant linear relationship with the flipper length
0.181 times the body length at all ages represented in this sample (142
cm. fetus to 535 cm. adult). Growth of the flipper must therefore pro-
ceed at the same rate as growth of the body. These findings confirm
those of Sergeant (1962b), who concluded on the basis of four flippers
that the growth of G. macrorhyncha flippers occurred at the same rate
as body growth.
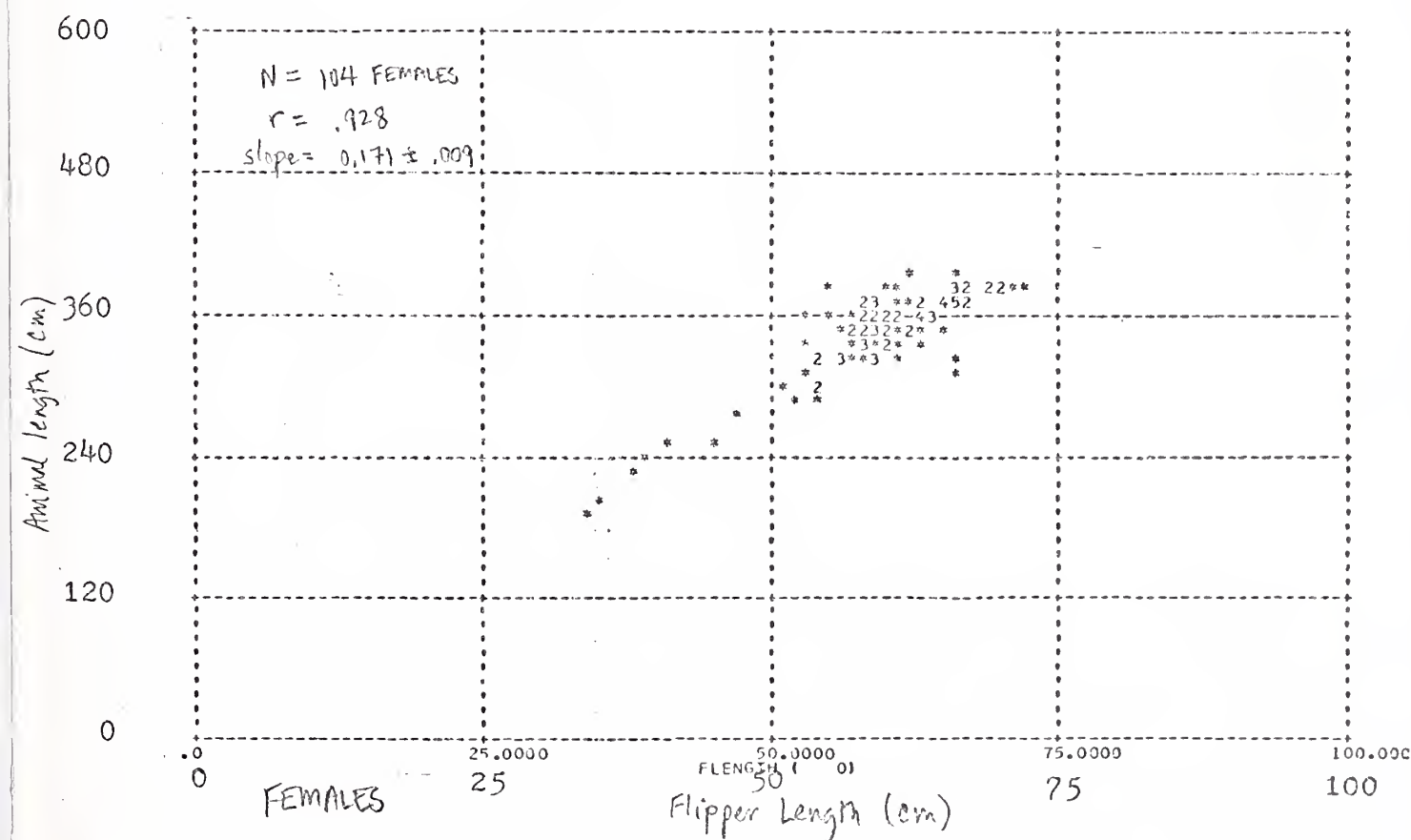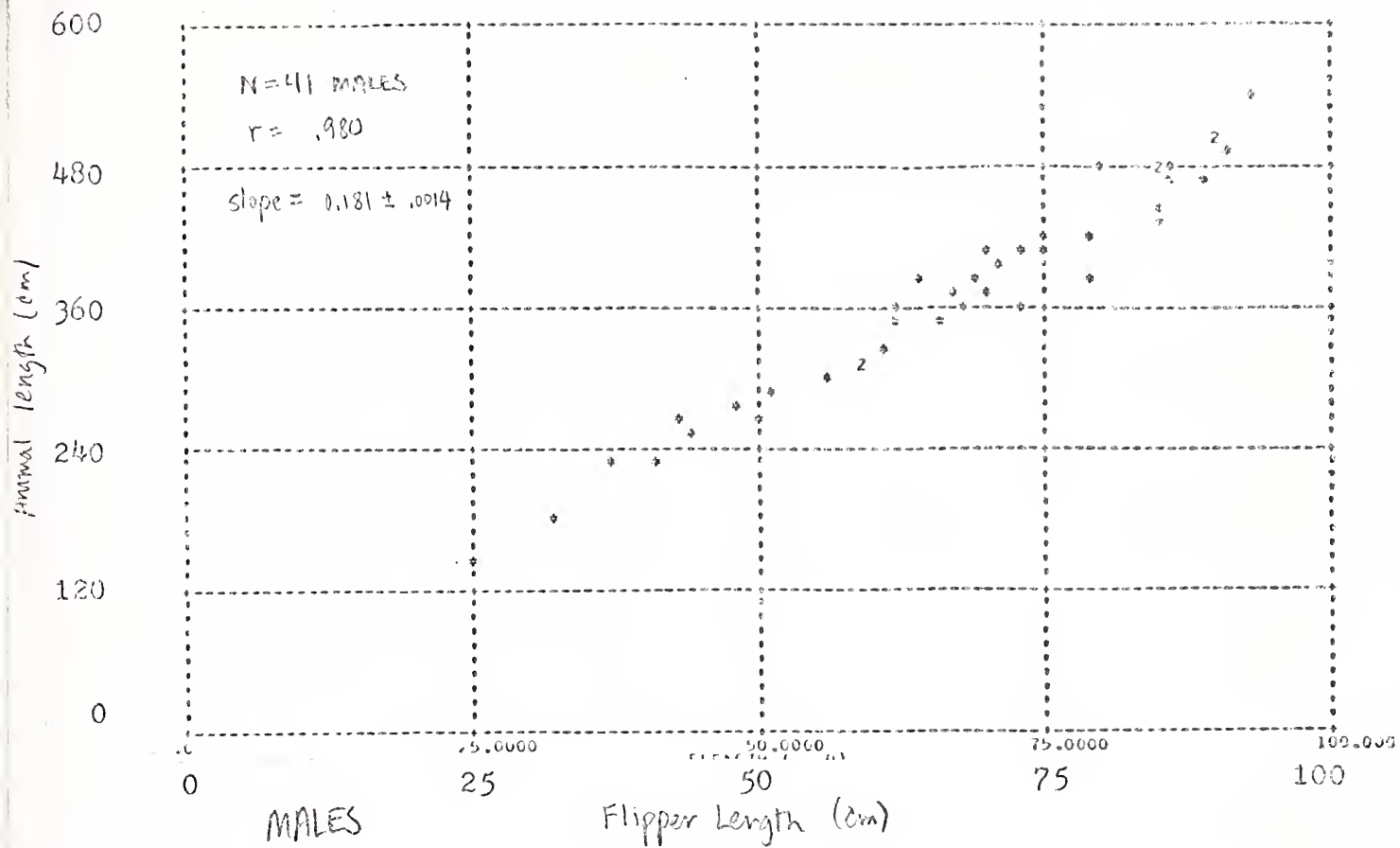
Graphs 1 and 2: Animal length vs flipper length
   NOTE: Digits on graph represent number of observations at that point.
      " X " = more than ten observations

Graph 2 shows the same relationship for females. Similar analysis revealed a slightly lower quality linear relationship; r = .928, slope = 0.171 ± 0.009 (SE), and t = 180 for 104 animals. The lower r-coefficient suggest that flipper length may be determined in part by factors other than animal length. The different slopes indicate that females have a slightly shorter flipper than do males at any given animal length.

The plot of flipper length against animal weight in graph 3 suggests an exponential relationship. Since flipper length is linearly related to animal length, and animal length cubed is proportional to animal weight, theoretically (McMahon 1973, Thompson 1961) and experimentally in this study (graph 4), we should expect flipper length cubed to be proportional to animal weight. This is confirmed in graph 5. Comparing these data with those for females shown in graphs 6, 7, and 8, it is obvious that there is much greater variation in weight at any given animal or flipper length in females than in males. It is probable that the female weight varies with the reproductive status of the individual, e.g., with pregnancy or lactation. Unfortunately no reproductive data are available for those of the sample with weight data, and no weight data are available for those with reproductive data.

Humerus, Radius and Ulna

In the youngest available flipper, a 142 cm. male fetus (figure 5), the primary ossification centers of the three long bones are already well developed. The proximal and distal humeral, humeral tubercle, and proximal radial and ulnar secondary centers all must develop during late fetal life, since these are absent in the specimen above but well-developed in newborn specimens C-186 a 223 cm. male (figure 6), and C-93, a 226 cm.
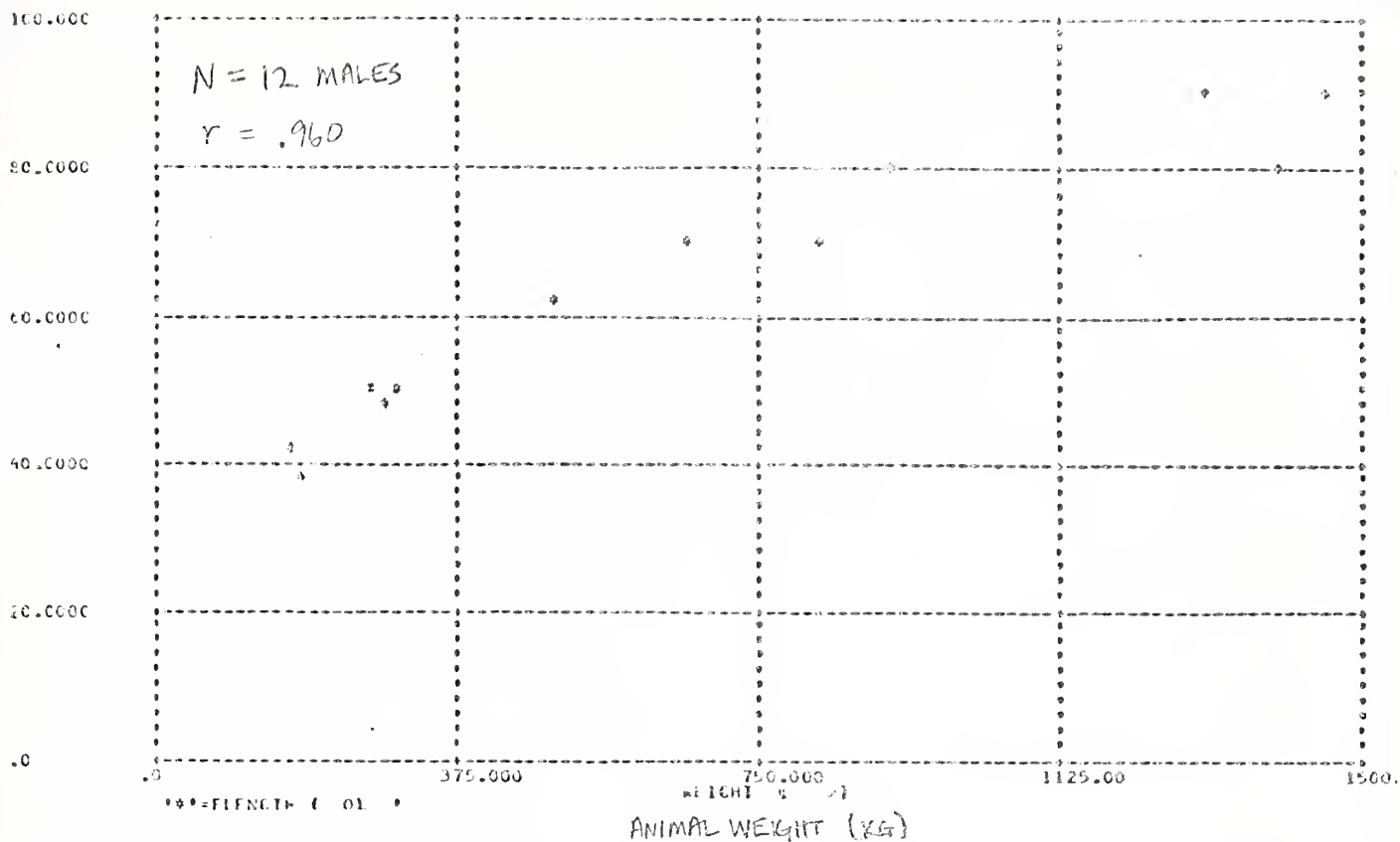
Graph 3 : MALE FLIPPER LENGTH vs ANIMAL WEIGHT
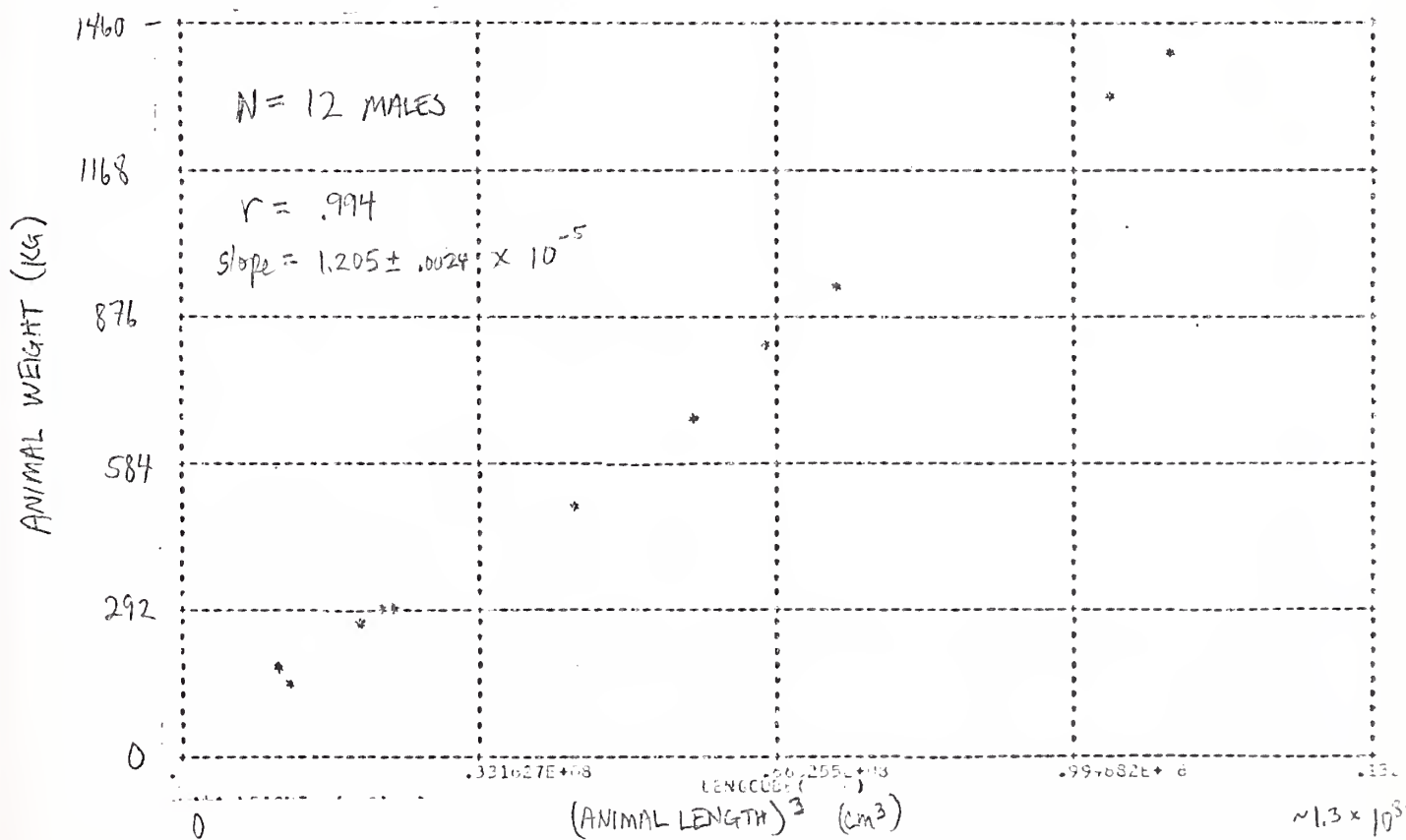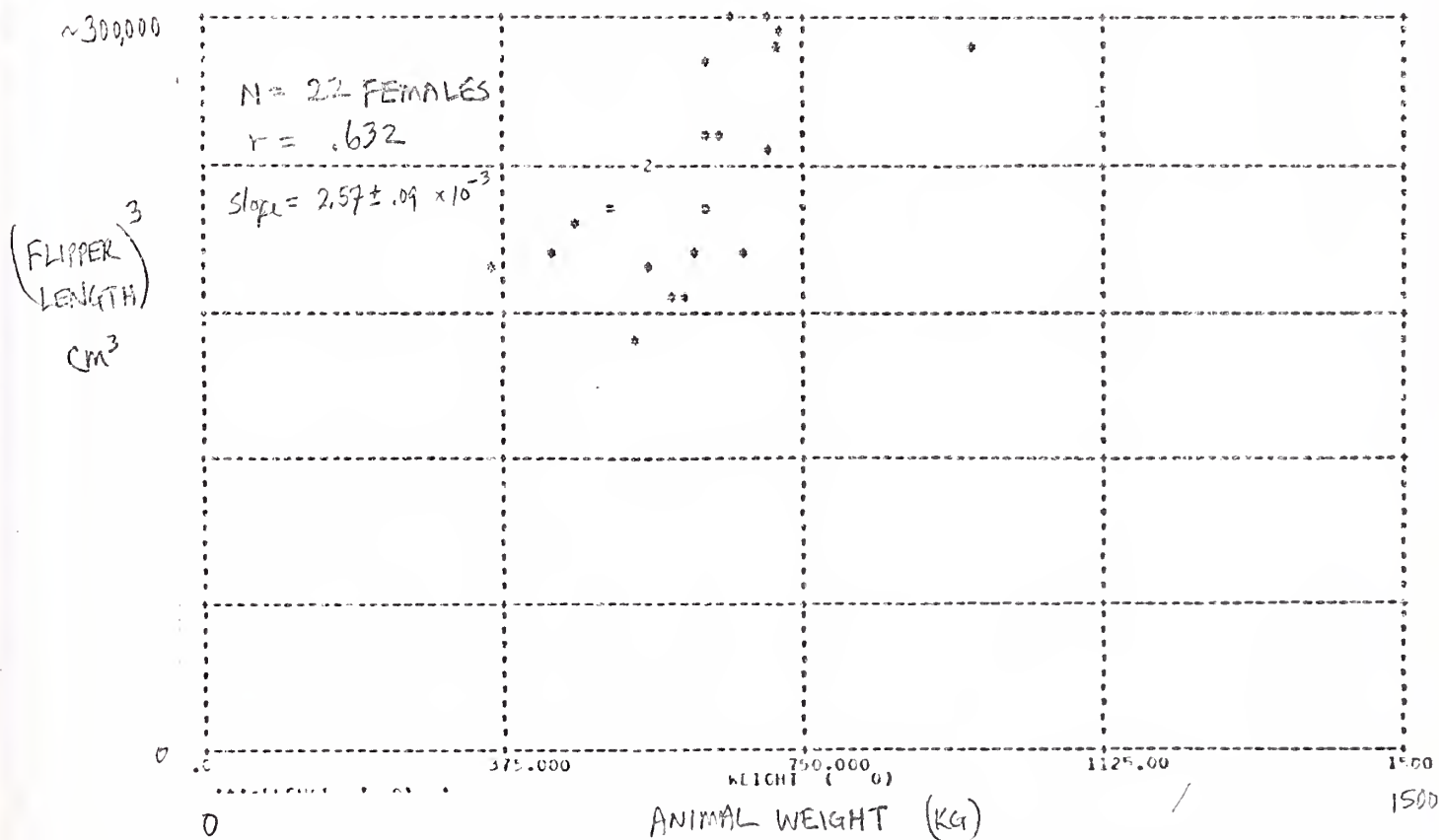

Graph 4 : WEIGHT vs ANIMAL LENGTH CUBED.
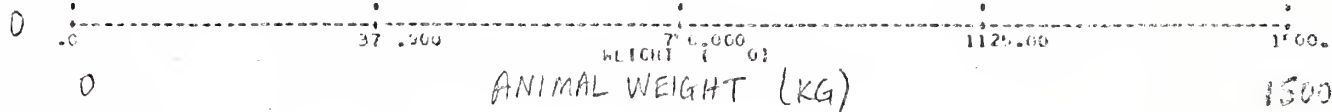
Graph 5: MALE FLIPPER LENGTH CUBED VS ANIMAL WEIGHT
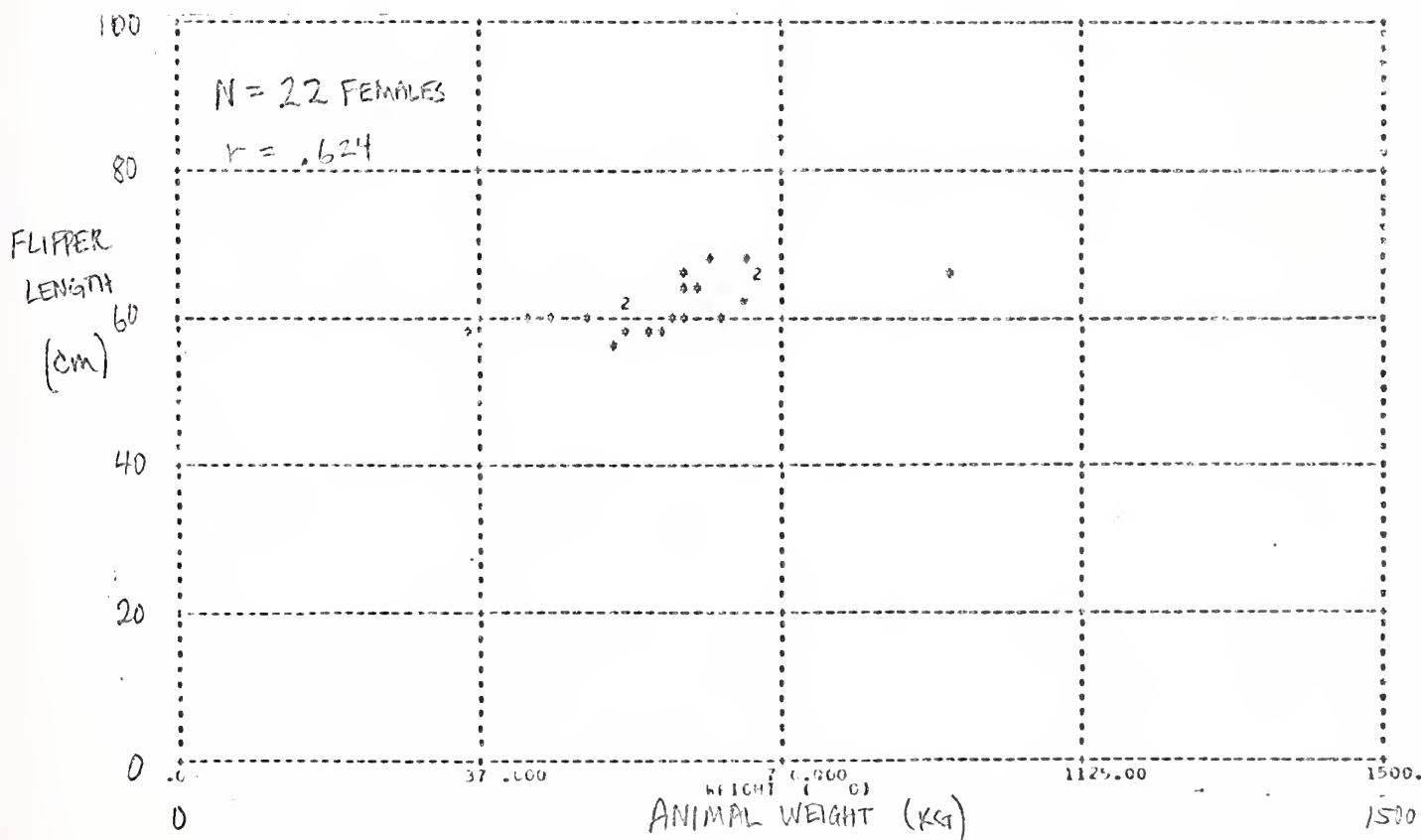
Graph 6: FEMALE FLIPPER LENGTH VS ANIMAL WEIGHT
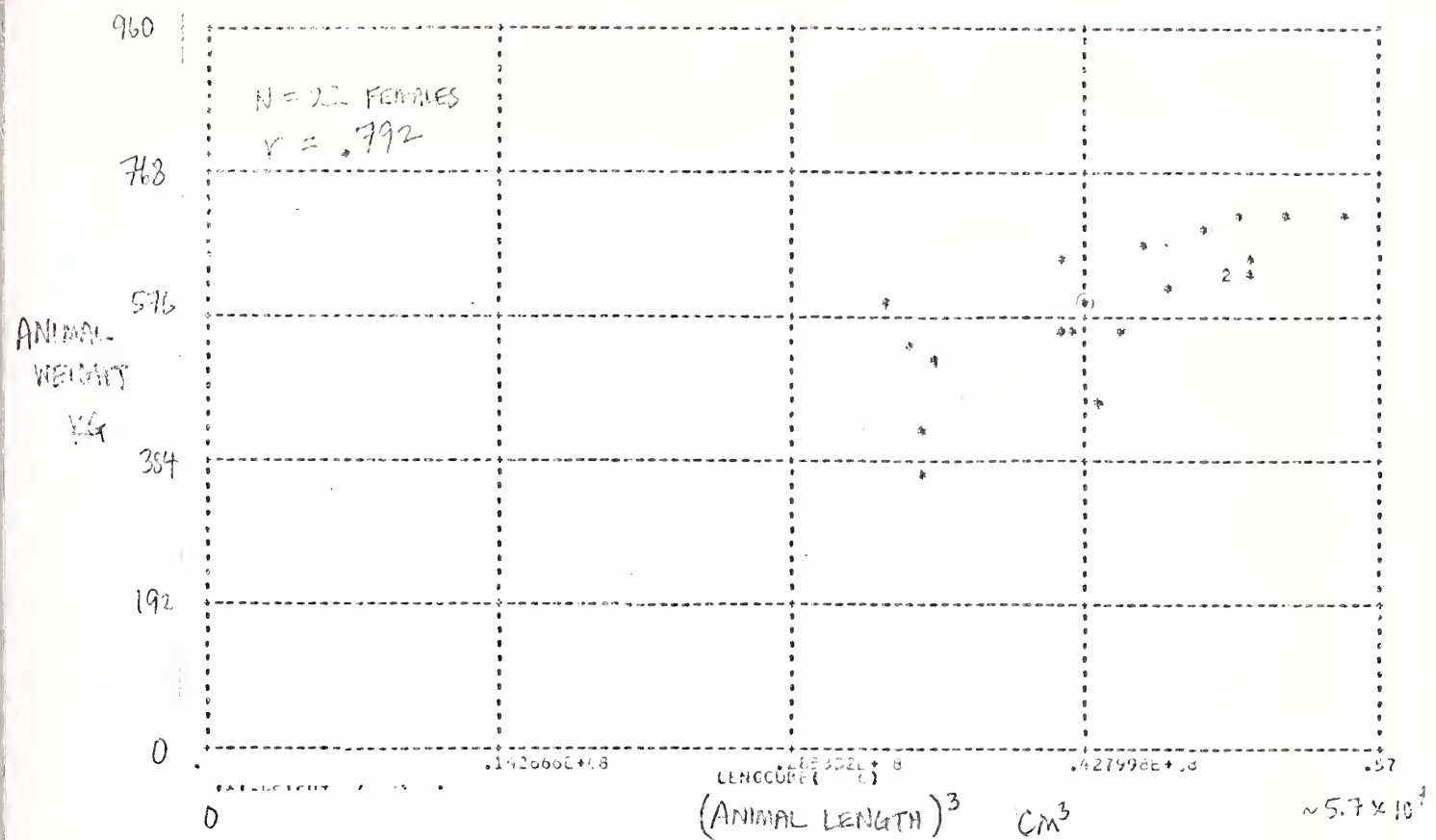
Graph 7: ANIMAL WEIGHT VS ANIMAL LENGTH CUBED; FEMALES

Graph 8: FEMALE FLIPPER LENGTH CUBED VS ANIMAL WEIGHT

female. The humeri, radii, and ulnae of the series of sectioned speci-
mens demonstrate various degrees of epiphyseal development and maturity.

Figures 6 through 11 show gross sections of the proximal humerus.
Figure 6 demonstrates that the proximal humerus develops from not one,
as previously reported, but two secondary ossification centers; one in
the humeral head proper, and one in the tubercle of the humerus. The
humeral tubercle center appears less well-developed than the humeral head
center, with a greater proportion of the epiphysis remaining cartilaginous.
Like the trochlea and the capitulum in the human, these two centers then
coalesce to form a single center (figure 7, 8, 9) which then undergoes
fusion to the metaphysis in the maturing flipper (figure 10, 11). It
is clear that the distal radial epiphyseal center also develops from
two ossification centers (figure 6, 7) which coalesce during the first
year of life. The distal ulnar epiphysis develops similarly, but does
so slightly later than does the radial center. To my knowledge, this
also has not been previously reported to occur in cetaceans. -

The order of fusion of the epiphyseal centers observed in these
samples is: distal humeral, proximal ulnar, proximal radial, these
three nearly simultaneously; then the united proximal humeral center;
then the distal ulnar followed very shortly by the distal radial cen-
ter. It was found that the various phases of radial and ulnar epiphyseal
maturity (as defined above in the methods section of this study) followed
a predictable pattern:

1. Proximal radial and ulnar centers 'developed' and physes 'open'.
2. Distal radial center 'appearing' or 'developing'.
3. Distal ulnar center 'appearing' or 'developing'.
4. Distal radial center 'open'.

5. Distal ulnar center 'open'.

6. Proximal radial and ulnar physes 'joined'.

7. Proximal radial and ulnar physes 'closed'.

8. Proximal radial and ulnar physes 'fused'.

9. Distal radial and ulnar physes 'joined'.

10. Distal radial and ulnar physes 'closed'.

11. Distal radial and ulnar physes 'fused'.

With very few exceptions, both male and female flippers followed this progression of arbitrary stages of radioulnar maturity. The few flippers which did not fit this pattern well showed overlap between stages 8 and 9; i.e., fusion of the proximal centers was not yet complete but closure of the distal centers had begun. Examples of flippers at various radioulnar stages are C-186 at RU stage 2, C-161 at RU stage 8, and C-150 at RU stage 11.

The radioulnar stage is plotted against the flipper length for male flippers in graph 9 and for female flippers in graph 10. Comparing the two plots, it is evident that females are at a higher radioulnar stage (i.e. are more mature) at any given flipper length than are males; and that females begin radioulnar maturation at shorter flipper lengths. For example, a 55 cm. female flipper will be in the terminal phases of closure of the distal radial and ulnar physes; while a male flipper of the same size may just have developed mature distal radial and ulnar epiphyses, and may not reach the same stage of flipper maturity until it is 80 cm. long. Female flippers appear to have somewhat more variation in maturity at a given length than do male flippers, especially at lengths from 50 to 65 cm. Thus for female flippers in this size range (which comprise the better part of this sample) the radioulnar stage should serve as a better indicator of physical maturity than would flipper size.
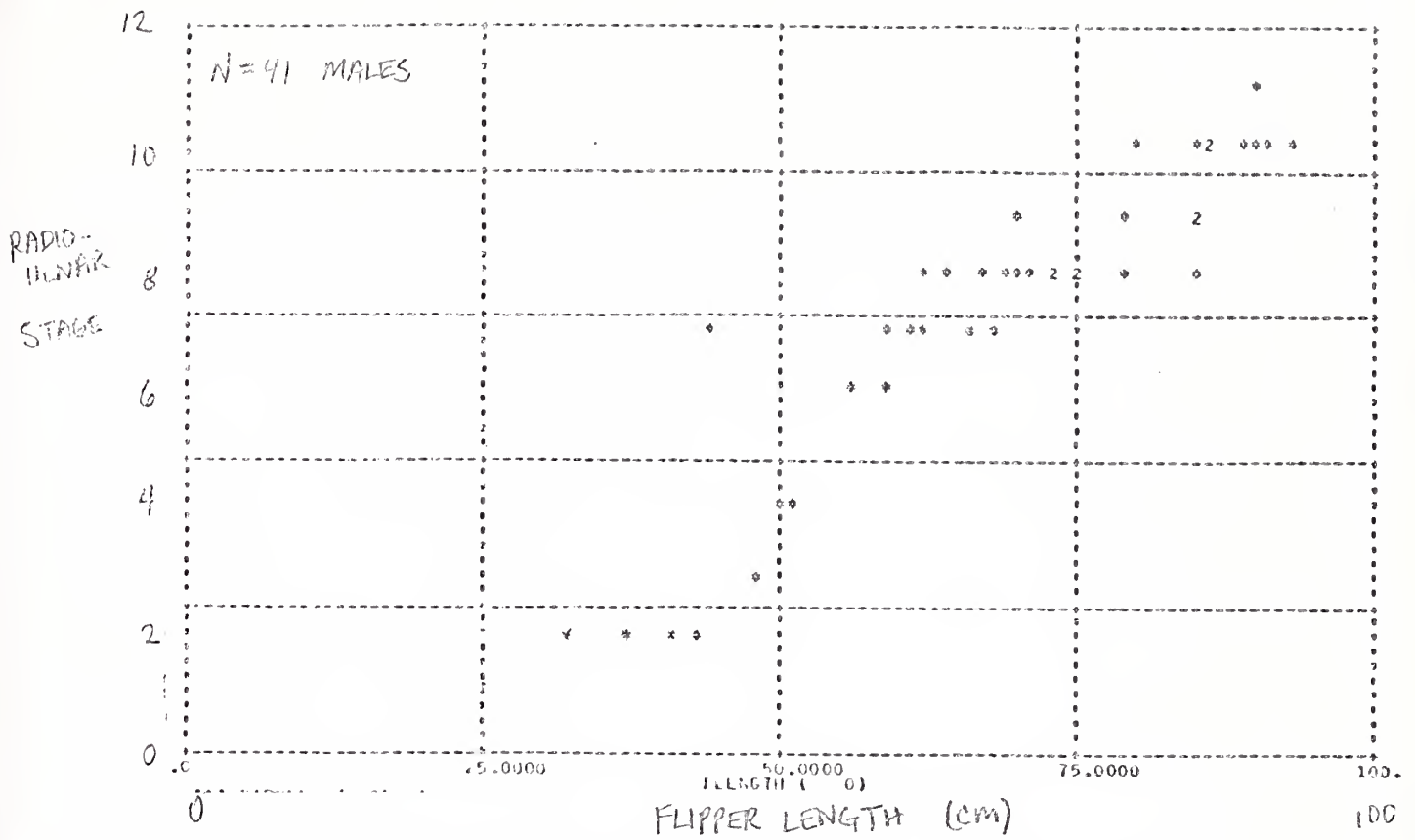
Graph 9: MALE RADIOULNAR STAGE vs FLIPPER LENGTH
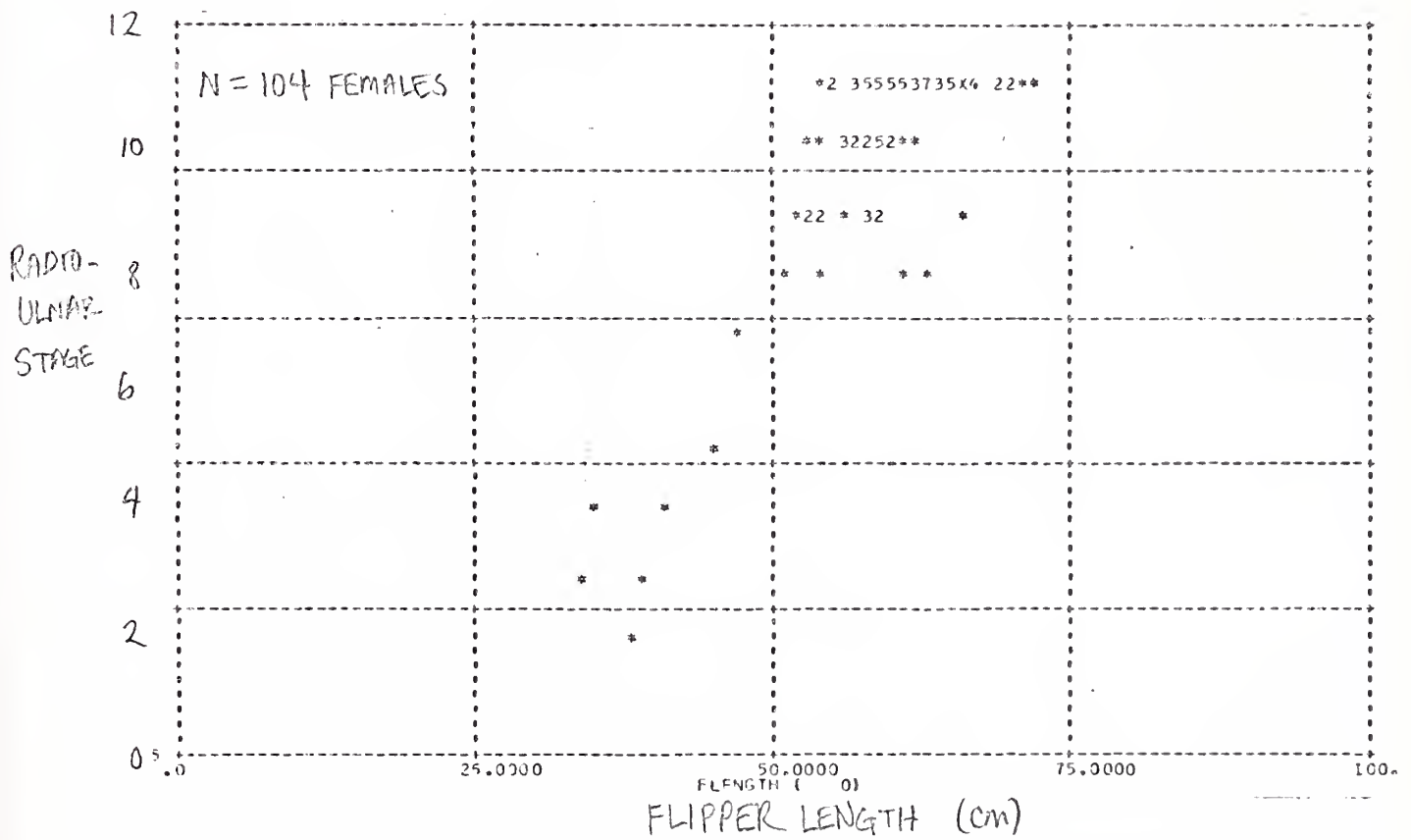
Graph 10: FEMALE RADIOULNAR STAGE vs FLIPPER LENGTH

Carpus

In G. macrorhyncha there is considerable animal-to-animal and flipper-to-flipper variation from the basic theme of three proximal and three distal carpals. The proximal row consists of a radial, an intermediate, and an ulnar carpal, while the distal row is usually called C1, C2, and C3 from radialmost to ulnarmost. The sectioned flippers illustrate some of the variations seen in the carpus of this species, and the radiographic survey provided an opportunity to investigate the frequency with which these variations are encountered. Specimen C-184 (figure 10) demonstrates a C1 in which the distal portion has the radiographic and gross appearance of a tubular bone rather than the polygonal irregular shape of a typical carpal bone. This "hybrid C1" was present in 2 of 43 male animals and 5 of 105 female animals. In only one of these seven animals were both flippers examined, and this animal had this variant bilaterally. The possibility that this "hybrid C1" represents a fusion of two originally separate elements, i.e., a C1 and a short first metacarpal, must be considered, but there is no radiographic or anatomic evidence to support this, and histologic examination is still pending.

Another variant is the presence of an accessory carpal in the proximal row located between and often synostotic with either the radial carpal or the intermediate carpal or both. This accessory carpal is probably homologous to the central carpal seen in other mammalian species and which has been reported to occur in this species by Kükenthal (1888a, b). In specimen C-150 (figure 11) this central carpal can be seen, completely fused to the intermediate. Radiographic evidence of a central carpal was seen in 2 of 43 males and 4 of 105 females. Three of the six

had both flippers radiographed and one of these three had bilateral accessory carpals. Four of the six had their central carpals fused to other carpals; two to the intermediate, one to the radial carpal, and one to both. Kükenthal had emphasized that the central carpal when it occurs always fuses with the intermediate in the grown animal. All six animals in this study with central carpals were mature by radio-ulnar stage.

An extra carpal in the distal row displacing the fourth metacarpal distally was seen in one flipper, C-184 (figure 10).

Three animals had only five ossified centers in the carpus, but two of these were very young animals; a 142 cm. male fetus with bilaterally absent ulnar carpal centers by x-ray, and a 236 cm. female calf with an absent CI center on the left but a CI center just appearing on x-ray on the right. These flippers indicate that the normal sequence of ossification of the carpus is probably variable, and the carpal centers usually appear by birth. One adolescent male (358 cm.) had a radiographically absent ulnar carpal, with a large C3 shifted proximally.

Carpal Secondary Centers

Flippers C-107, C-161, and C-184 (figures 8, 9, 10) demonstrate secondary ossification centers in some of the carpal bones of the flipper. Secondary centers of ossification in the carpus have not been reported for any animal except for a single sentence by Flower (1876): "In the Physeter   many of the carpal bones, in addition to the usual central nucleus, have epiphyseal ossifications developed in the periphery of the carilage, which ultimately unite with the central pieces of bone".

The carpal "epiphyses" demonstrated in the gross sections were studied radiographically by noting their presence or absence at each element of the carpus and scoring those present for epiphyseal maturity using the same criteria as was used for the other bones of the flipper. It must be emphasized that the interpretation of "epiphyseal" maturity in the carpus is a rather subjective process, and that the data presented here are meant only to serve as a general guide for the purposes of qualitative description, and not as an attempt at a mathematical formulation.

The carpal "epiphysis" initially appears as a small nodular density separated from the primary center of the carpal by not more than about one mm. of radiolucent space. As it develops, it assumes a flattened appearance, following the contours of and curving around the primary center. The well-developed center is rarely seen without some point of contact with the primary center; this is very probably a function of the projection of these elements onto the radiograph, and it should not be concluded without further investigation that "closure" of the "physis" occurs rapidly on radiographic evidence alone.

Which of the carpals develop secondary centers is variable, as is the position of the secondary centers relative to the primary center. Animals in which both flippers were examined generally but not always showed similar patterns of carpal secondary centers on both sides. Table 5 gives the number of male animals which developed secondary carpal centers, divided by carpal primary center and by stage of maturity; table 6 gives the data for females. A greater proportion of the female sample developed secondary centers than did the male sample, and those secondary centers tended to be more mature in females than in males. These differences are very probably reflections of the greater proportion of mature

TABLE 5

LOCATION AND MATURITY OF CARPAL
SECONDARY CENTERS IN 43 MALE G. MACRORHYNCHA.

Maturity of 2° centers	rad.	int.	Location uln.	C1	C2	C3
Absent	8	13	30	25	15	35
Appearing	2	2	1	4	0	2
Developing	1	1	0	1	2	0
Open	6	0	0	4	2	0
Joined	17	5	2	4	9	0
Closed	8	12	1	4	11	3
Fused	1	9	7	1	4	3
1° center absent	--	-	2	-	-	-

TABLE 6

LOCATION AND MATURITY OF CARPAL

SECONDARY CENTERS IN 108 FEMALE G. MACRORHYNCHA.

Maturity of 2° centers	rad.	int.	Location uln.	C1	C2	C3
Absent	7	9	36	8	8	29
Appearing	0	0	0	1	1	1
Developing	0	0	0	4	0	0
Open	2	1	0	8	1	0
Joined	11	3	1	10	1	0
Closed	20	11	4	18	16	3
Fused	68	84	67	58	81	75
1° center absent	-	-	-	1	-	-

animals in the female sample. In both males and females secondary car-
pal centers are present least often in the ulnar carpal and in C3, and
more often in the other carpals. In both sexes, secondary centers at
the radial carpal and at C1 tended to mature more slowly than those at
other carpals.

Considering the variability of the presence and of the location
of these carpal "epiphyseal" centers, and the shape of the mature carpal
bone, it would seem that a true physis capable of longitudinal growth
would serve no purpose in the cetacean carpus. In addition, in some
specimens (e.g., C-184, figure 10) the carpal "epiphyseal" center ap-
pears to completely encircle the primary center in the plane of the sec-
tion. In these cases, it is difficult to imagine the geometry of growth
at the "physis". Whether these centers represent epiphyses in the strict
sense or whether these could be a pseudoepiphysis similar to that seen
in the phalanges of cretins, or perhaps another structure different from
both of these, can only be decided on study of histologic sections.

Preliminary examination of paraffin sections of C3 from specimen
C-184 reveals a secondary ossification center in the process of fusion
with the primary center, but still separated from the primary center in
areas by sections of cartilaginous growth plate. Unfortunately, because
of the large size of the specimens, great technical difficulties were
encountered in cutting paraffin sections, and those sections which were
produced are of technically poor quality. While these sections confirmed
the radiographic and gross findings of carpal secondary centers, a more
complete histologic study of the carpal epiphyses must await the prepara-
tion of better quality sections by celloidin processing, a process while
unfortunately requires approximately one year.

Digits

The phalangeal formula (with metacarpals included) for G. macro-
rhyncha is I: 1, II: 7 - 9, IV: 2, V: 1, based on the radiographic
survey of both the Yale series and the Smithsonian series. An occasional
flipper may fall outside this range. The factors (if any) which contri-
bute to the variations in phalangeal count remain unclear. The phalan-
geal count for digit II is plotted against flipper length in graphs 11
and 12, and against radioulnar stage in graphs 13 and 14. It is apparent
that there is no consistent relationship between the phalangeal count
and flipper growth or radioulnar maturity; the variation in the number
of phalanges in digit II appears independent of growth or maturity in
postnatal animals. The same can be demonstrated for the counts of the
other digits. These samples, which are considerably larger than those
used by earlier authors, refute the "law" of Phalangenreduktion of Kûken-
thal (1888a,b) and Künze (1912) as well as Weber's (1888) theory that
the phalangeal count increases with postnatal growth. These do not dis-
prove the possibility that some flippers add phalanges while equal num-
bers of flippers resorb phalanges, but this seems hardly likely. The pre-
natal development of phalangeal centers and changes (if any) in the pre-
natal phalangeal count still require clarification.

The bipolar epiphyseal ossification centers of the metacarpals and
phalanges can be seen in the gross sections and radiographs in figures
7 through 11. The metacarpals and proximal phalanges develop typical ap-
pearing epiphyseal ossification centers, with radiographically and
grossly typical appearing cartilaginous physes separating the epiphyseal
center from the primary center. However, in the more distal phalanges,
the epiphyseal centers do not show radiographically typical epiphyseal
centers of ossification (figure 12). Instead, multiple small nodular
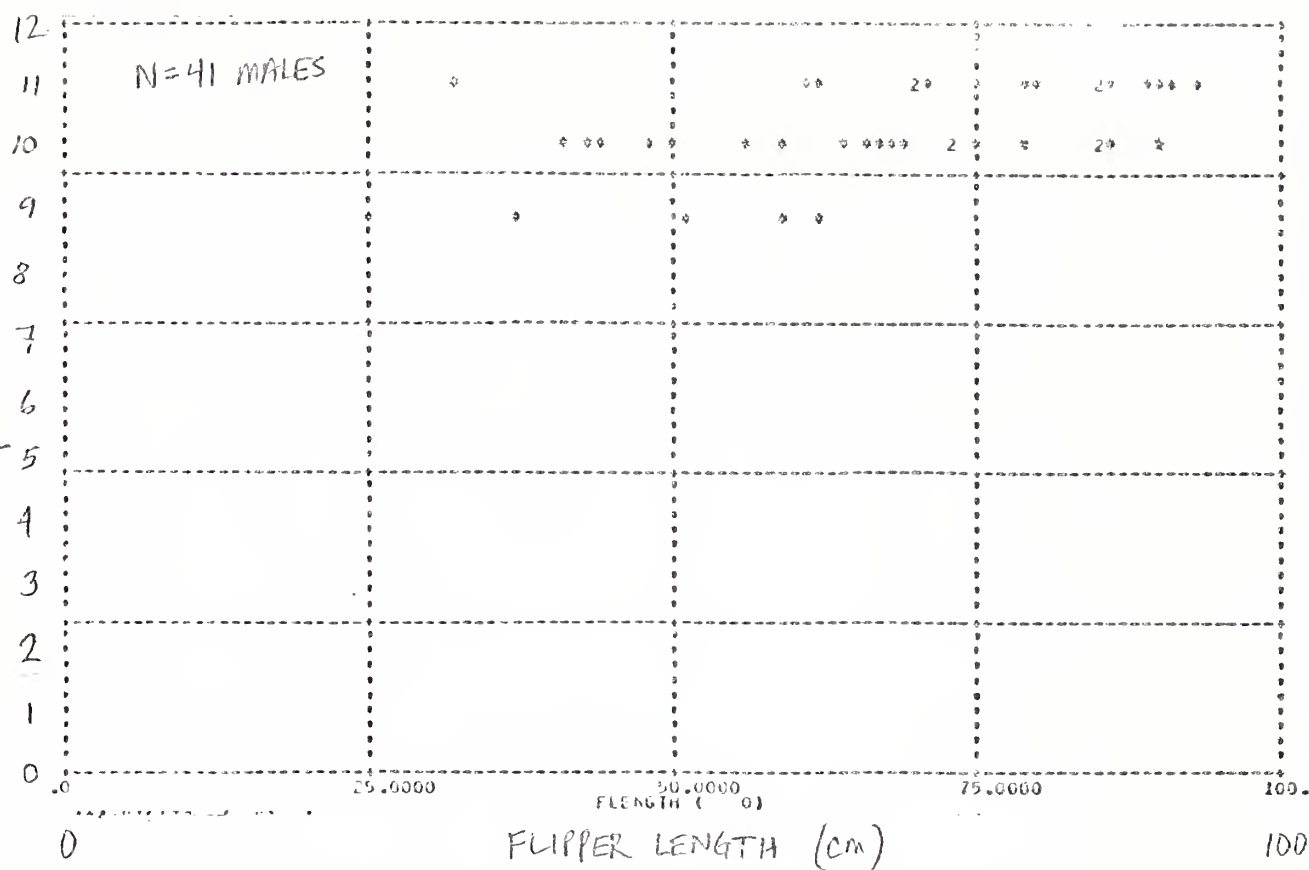
Graph 11: MALE PHALANGEAL COUNT VS. FLIPPER LENGTH
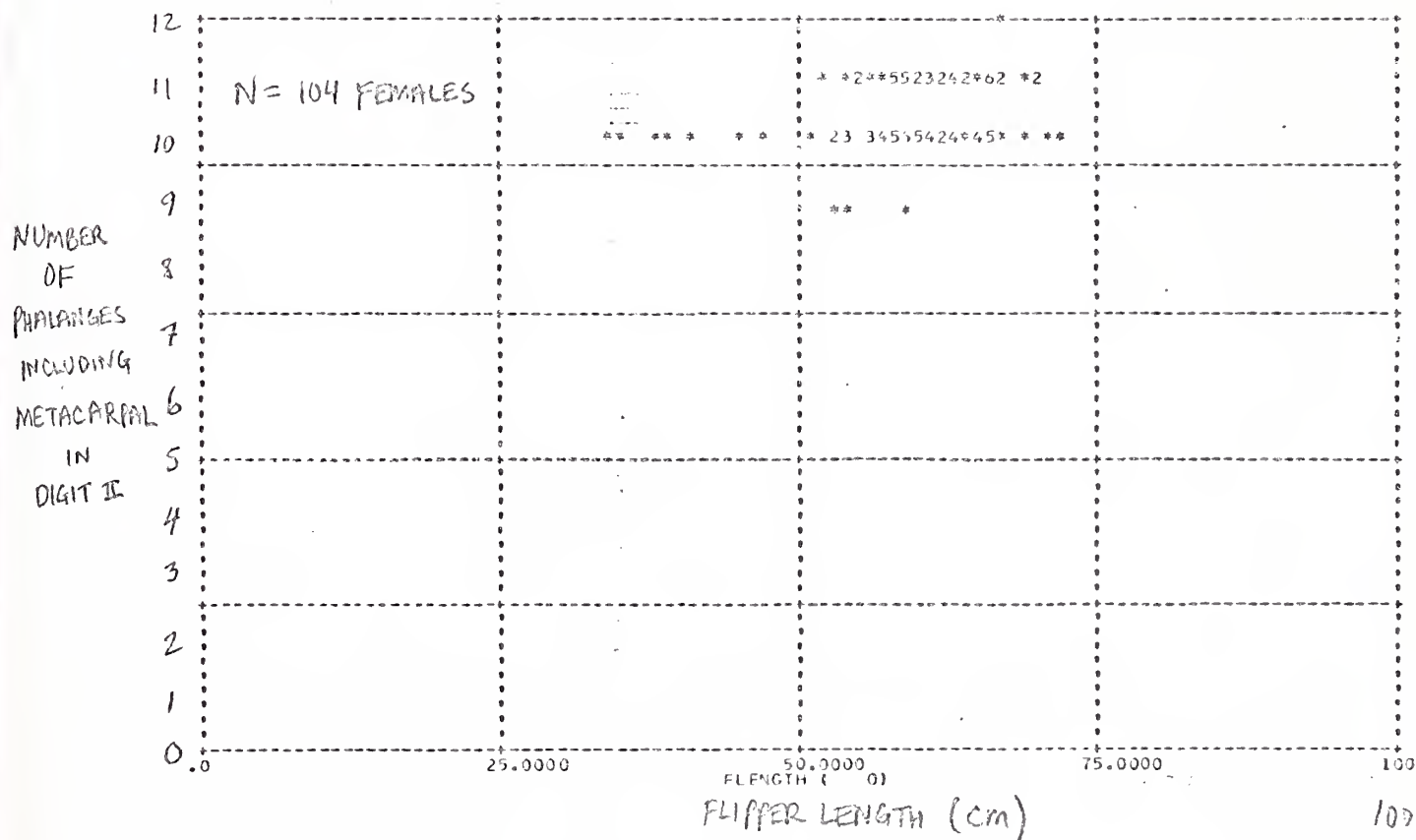
Graph 12: FEMALE PHALANGEAL COUNT VS FLIPPER LENGTH
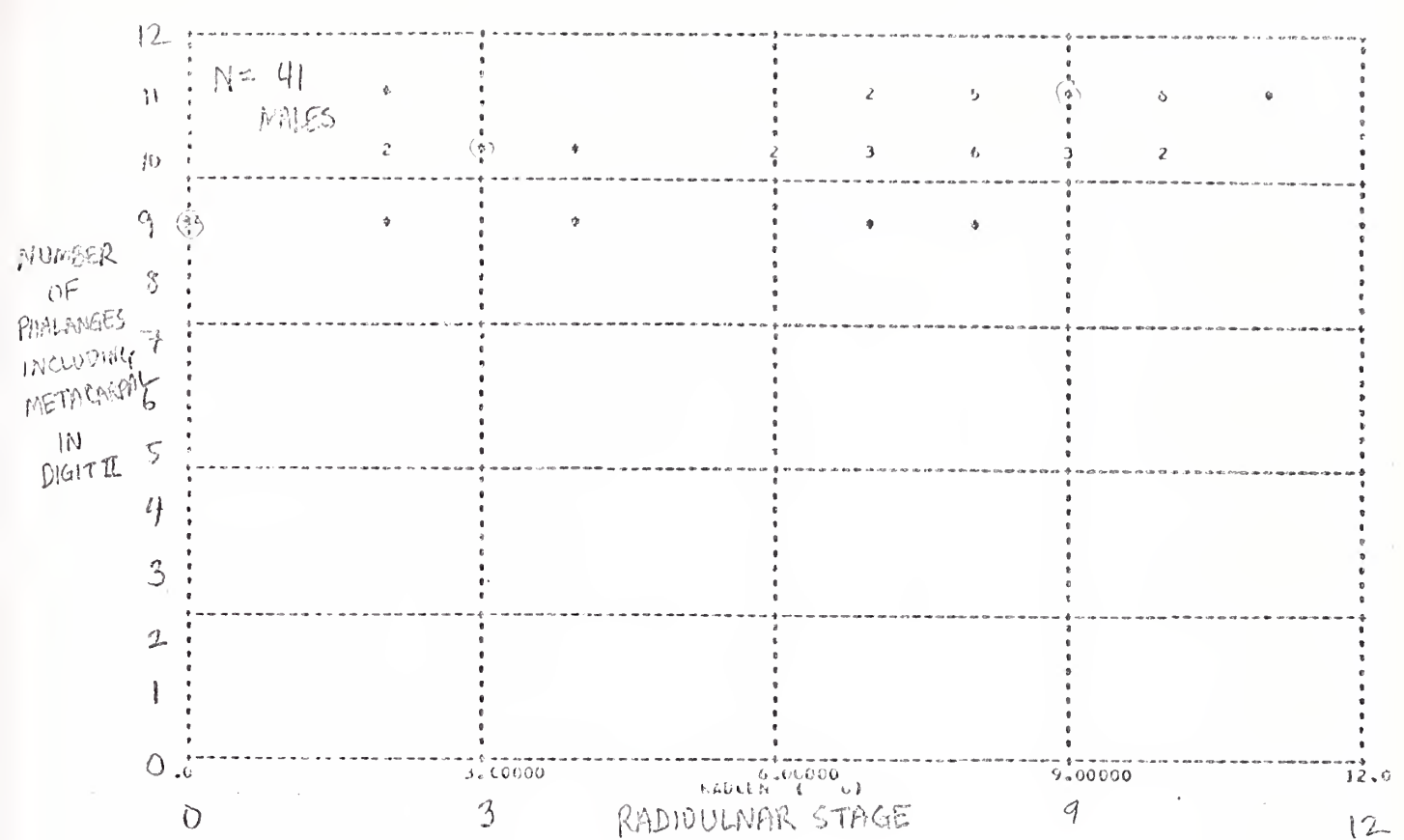
Graph 13: MALE PHALANGEAL COUNT VS. RADIOULNAR STAGE
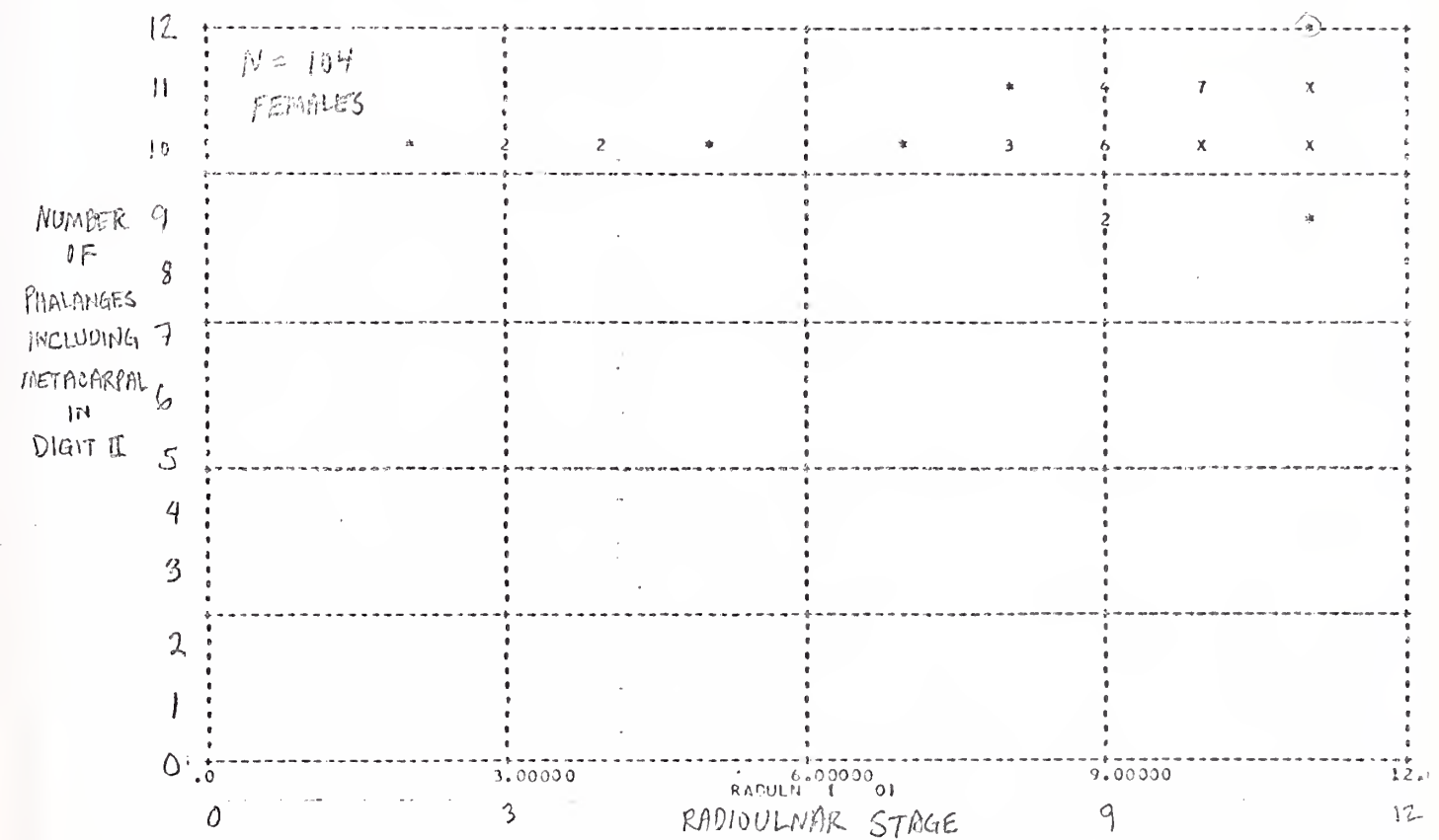
Graph 14: FEMALE PHALANGEAL COUNT VS. RADIOULNAR STAGE

ossifications develop, not always clearly separated from the primary center. As these epiphyseal centers mature, they increase in density, coalesce together and then fuse to the primary center. The net effect of these centers is to change the shape of the phalanx from a rounded nodule with convex or flat proximal and distal ends to a phalanx with concave ends. The terminal phalanges usually remain rounded nodules and very rarely develop epiphyseal centers, even in the most mature animals. The epiphyses develop first in the second digit, followed by third, fourth, first, and fifth digit.

Within each digit, the bony epiphyses appear first in the metacarpals, then in the phalanges in a proximal to distal succession. The gross sections and the radiographs of specimens C-104, C-107, and C-161 (figures 7, 8, 9) illustrate this sequence. Within each phalanx, the proximal epiphysis appears and develops before the distal center does, but rarely a distal center may be just visible without a proximal center.

In many of the Smithsonian series of radiographs, longitudinal cartilage canals were clearly visible in the metacarpals and phalanges traversing the physeal region, even in the presence of a radiographically well-developed bony epiphysis (figure 13). In a few instances, cartilage canals arising from the periphery of the epiphysis were visible radiographically, but these canals appeared smaller in caliber than the transphyseal canals. These findings were also observed on inspection of gross flipper sections. To my knowledge, this pattern of epiphyseal vascular anatomy has not been previously described for any species. In the human, transphyseal canals are absent once the epiphyseal center is fully developed and the subchondral plate has formed in the bony epiphysis. If these findings are confirmed on histologic examination this would constitute a significantly different mechanism of epiphyseal vascularization

from those previously described for other mammals.

In order to clarify the relationship between epiphyseal development in the digits, flipper growth, and radioulnar maturity, a series of plots are shown in graphs 15 through 18. Graphs 15 and 16 show the digital epiphyseal number (defined as the number of phalanges including the metacarpal in digit II with epiphyseal ossification centers on x-ray) plotted against flipper length for males and females. Both plots confirm that the number of phalanges with epiphyseal centers increases with growth; i.e., the epiphyseal ossification centers appear sequentially, and their number can be used as an indicator of digital maturity, as the radioulnar stage can be used to indicate radial and ulnar maturity. Comparing the sexes, we note that as with the radioulnar stage, digital epiphyseal development begins at shorter flipper lengths and is greater at any given flipper length for females than for males. Graphs 17 and 18 show that the relationships between epiphyseal development in digit II and the radioulnar stage for both sexes are approximately equivalent. The epiphyseal ossification centers of the second metacarpal appear while the distal radial and ulnar epiphyses are developing; bony epiphyses appear in the most proximal phalanx while the proximal radial and ulnar epiphyses are beginning the process of fusion; and so on. Similar relationships can be demonstrated for the phalanges of the third digit, with the following exceptions: the second and third metacarpals develop their epiphyseal centers nearly simultaneously, but the development of epiphyseal centers in the phalanges of digit III lags behind that of digit II. It is in any case clear that contrary to Felts' (1966) statement that only the very largest Globicephala ever develop phalangeal epiphyses, phalangeal epiphyseal ossifications develop in adolescence in both sexes.
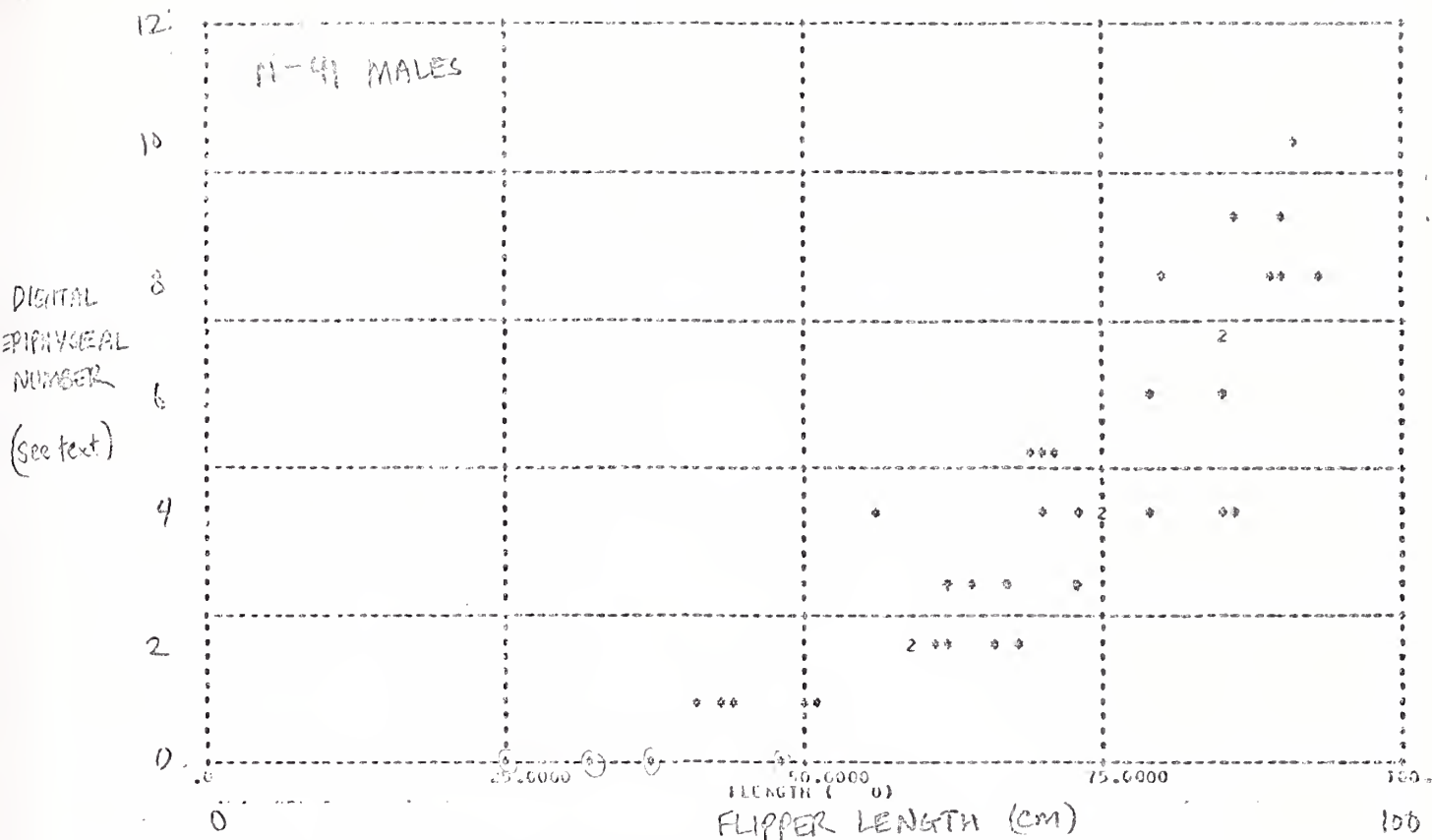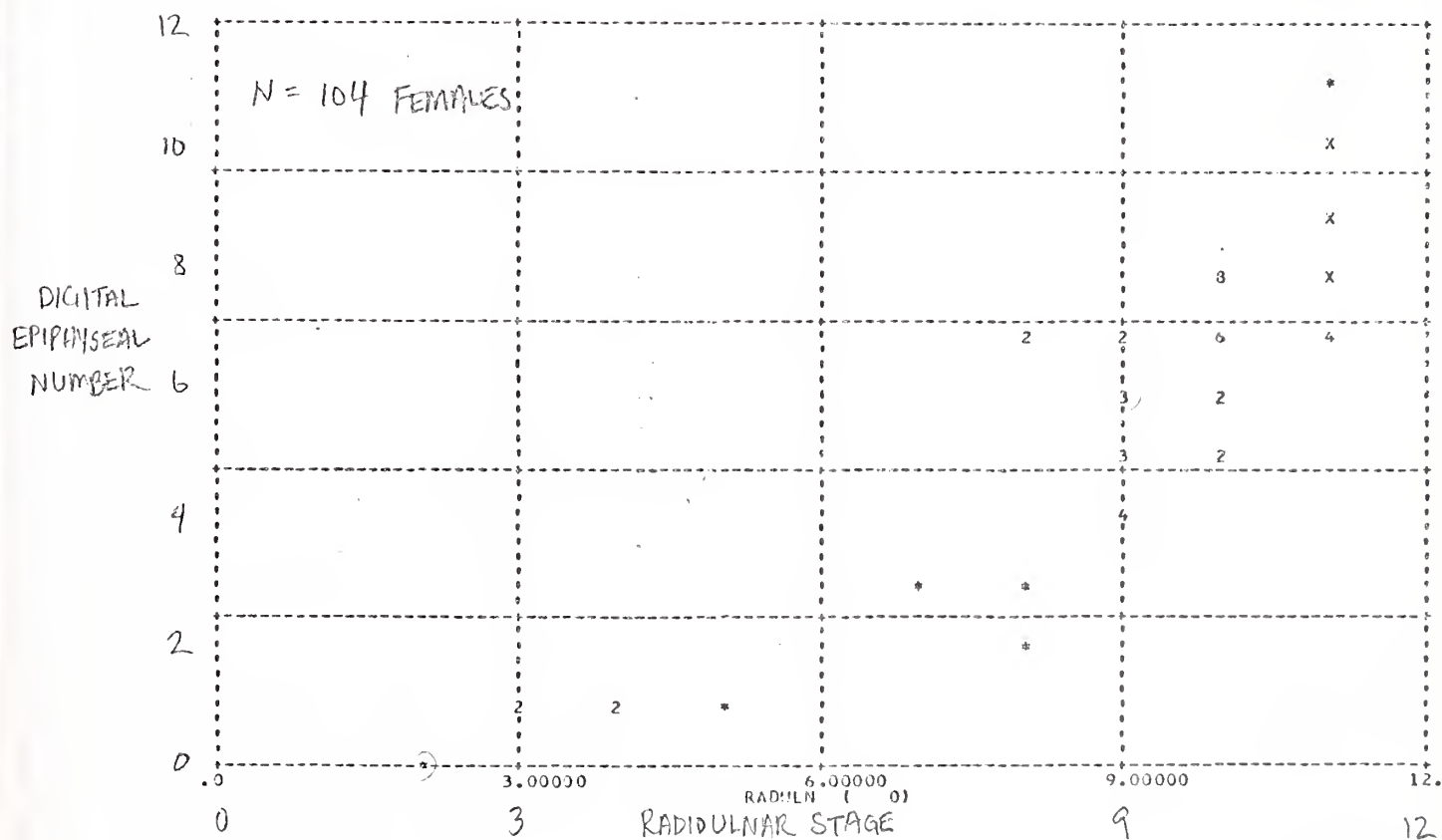
Graph 15: MALE DIGITAL EPIPHYSEAL NUMBER VS FLIPPER LENGTH
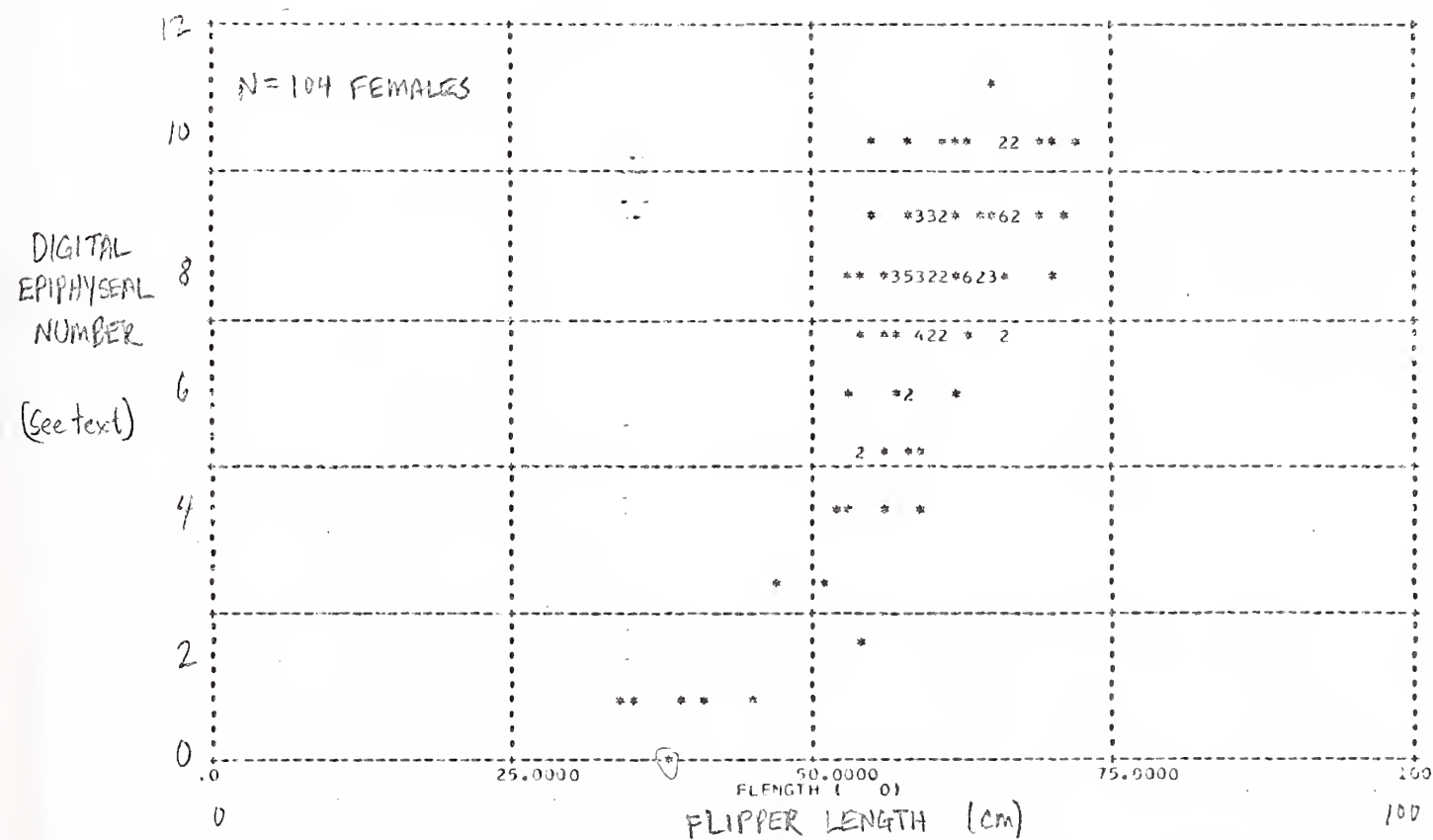
Graph 16: FEMALE DIGITAL EPIPHYSEAL NUMBER VS, FLIPPER LENGTH
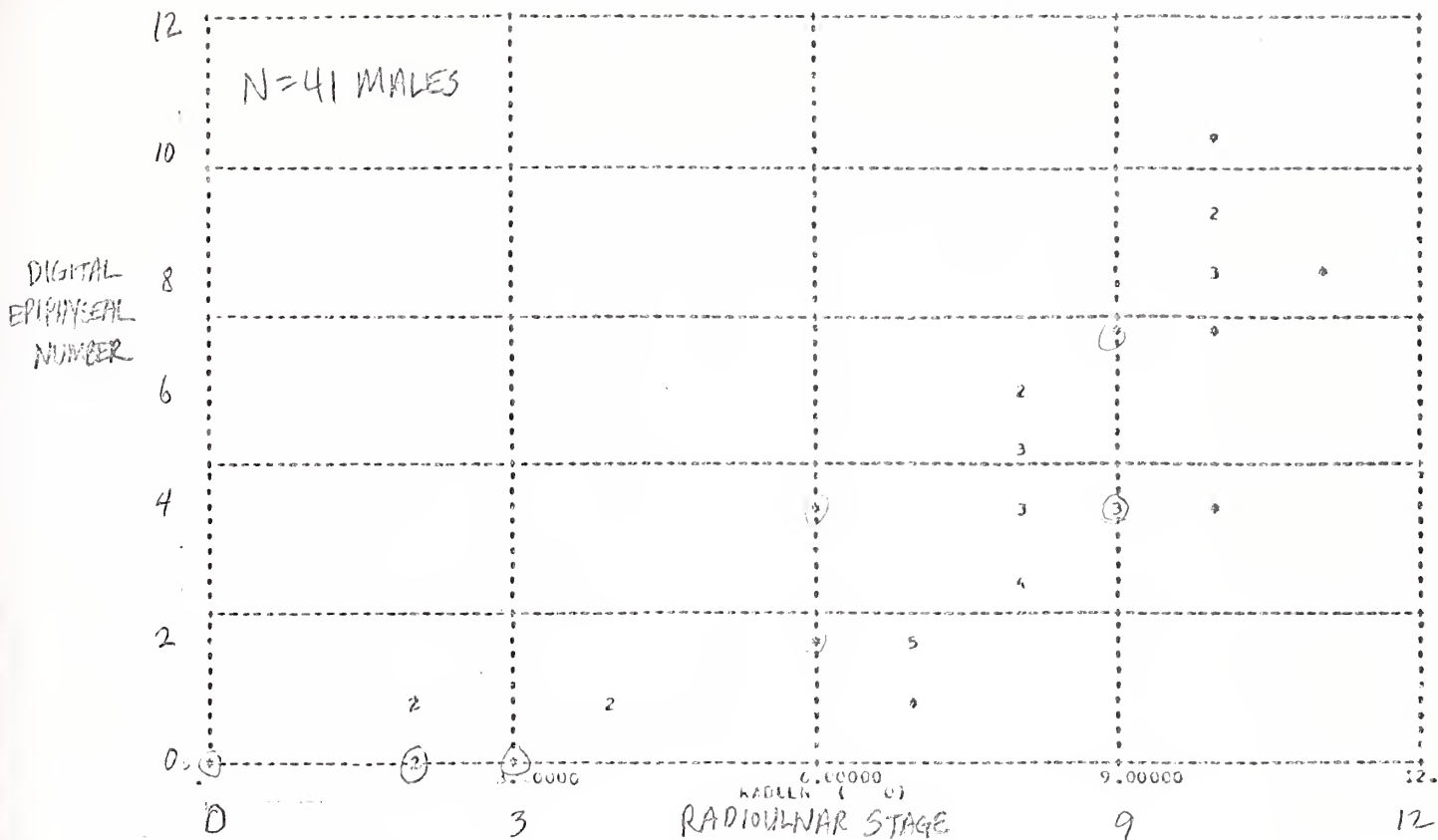
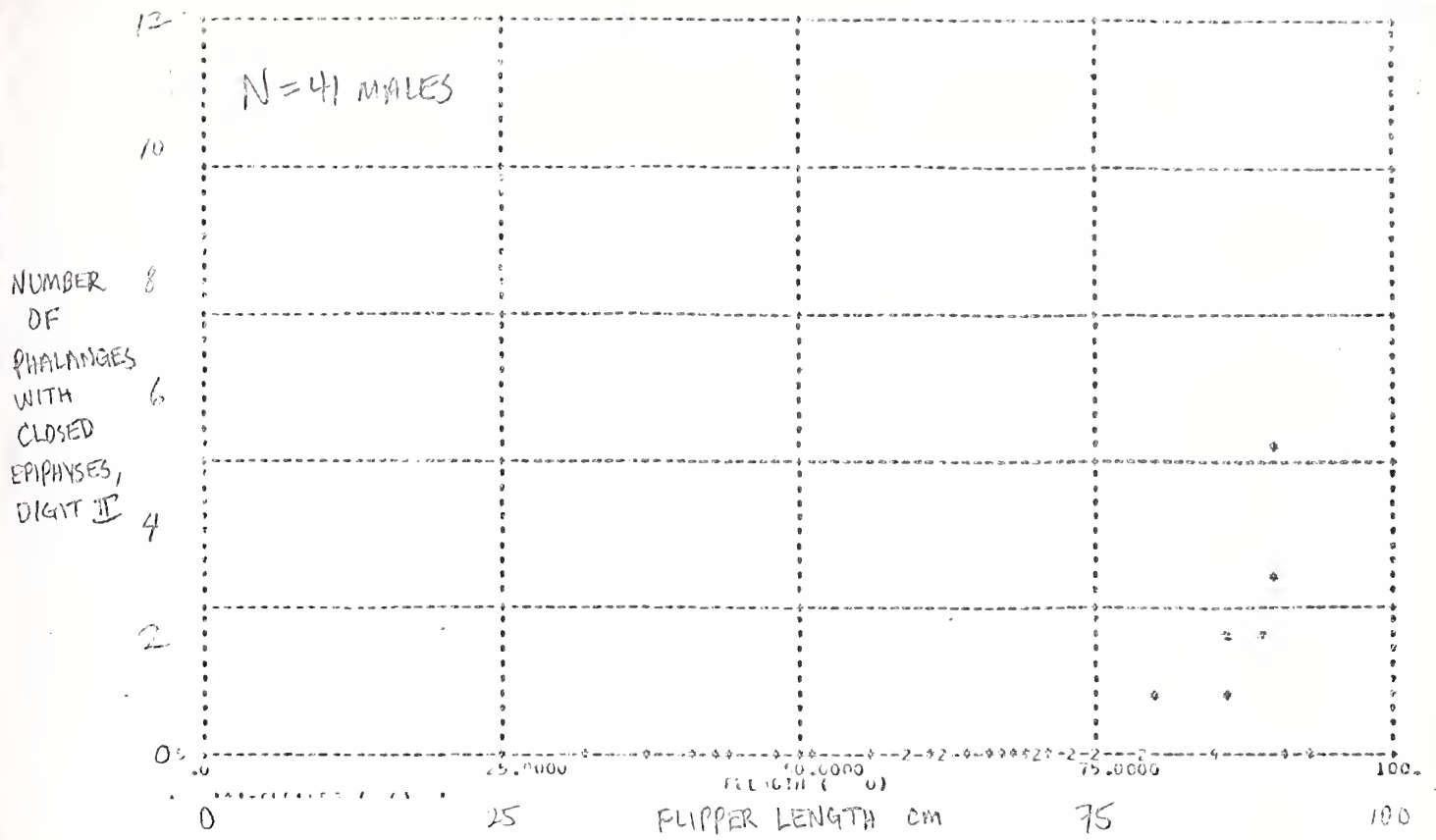Graph 17: MALE DIGITAL EPIPHYSEAL NUMBER vs. RADIOULNAR STAGE

Graph 18: FEMALE DIGITAL EPIPHYSEAL NUMBER vs RADIOULNAR STAGE

Graphs 19 through 22 show the relationship between closure of the digital epiphyses and flipper length, and between closure and the radioulnar stage. Closure of the digital epiphyses does not occur until after the distal radial and ulnar epiphyses have closed and flipper growth is complete. From graphs 19 and 21, it is clear that this sample of males contained very few who had matured to the stage of closure of the digital epiphyses; this probably reflects a bias in the sample of males used for this study.

Joints

Other than the glenohumeral joint, there was no evidence of synovial joints in these flippers. All the joints were immovable and appeared grossly to be fibrous joints between cartilage, with many fine fibers traversing the joint and connecting the elements to one another. These fibers are perhaps best seen in figure 10. No synchondroses were seen, nor were any "imperfect synovial joints" seen.

Figure 14 illustrates a Dermestid larvae cleaned flipper. The cleaned bony elements have been arranged in an approximately anatomic arrangement using a pre-cleaning radiograph as a guide. This flipper demonstrates a fully fused humeral-ulnar joint, as well as proximal radio-ulnar and ulnar carpal-fifth metacarpal fusions. Specimens C-184 and C-150 (figures 10 and 11) show earlier stages in the process of humeral-ulnar ankylosis. The fibrous tissue within the joint appears to be preserved while the articular cartilages of both bones are eroded away by advancing ossification from within each bone. Grossly, there is no evidence of inflammation. Based on the gross examination, this progressive fusion resembles the synostosis which occurs at the cranial sutures rather

Graph 19 (top):

N=41 MALES

NUMBER OF PHALANGES WITH CLOSED EPIPHYSES, DIGIT II

12
10
8
6
4
2
0

FLENGTH (0)

.0   25.0000   50.0000   75.0000   100.

0   25   FLIPPER LENGTH CM   75   100

Graph 19: MALE NUMBER OF PHALAGES WITH CLOSED EPIPHYSES IN DIGIT II
VS FLIPPER LENGTH

Graph 20 (bottom):

N = 104 FEMALES

NUMBER OF PHALANGES WITH CLOSED EPIPHYSES, DIGIT II

12
10
8
6
4
2
0

FLENGTH (0)

.0   25.0000   50.0000   75.0000   100

0   25   FLIPPER LENGTH CM   75   100
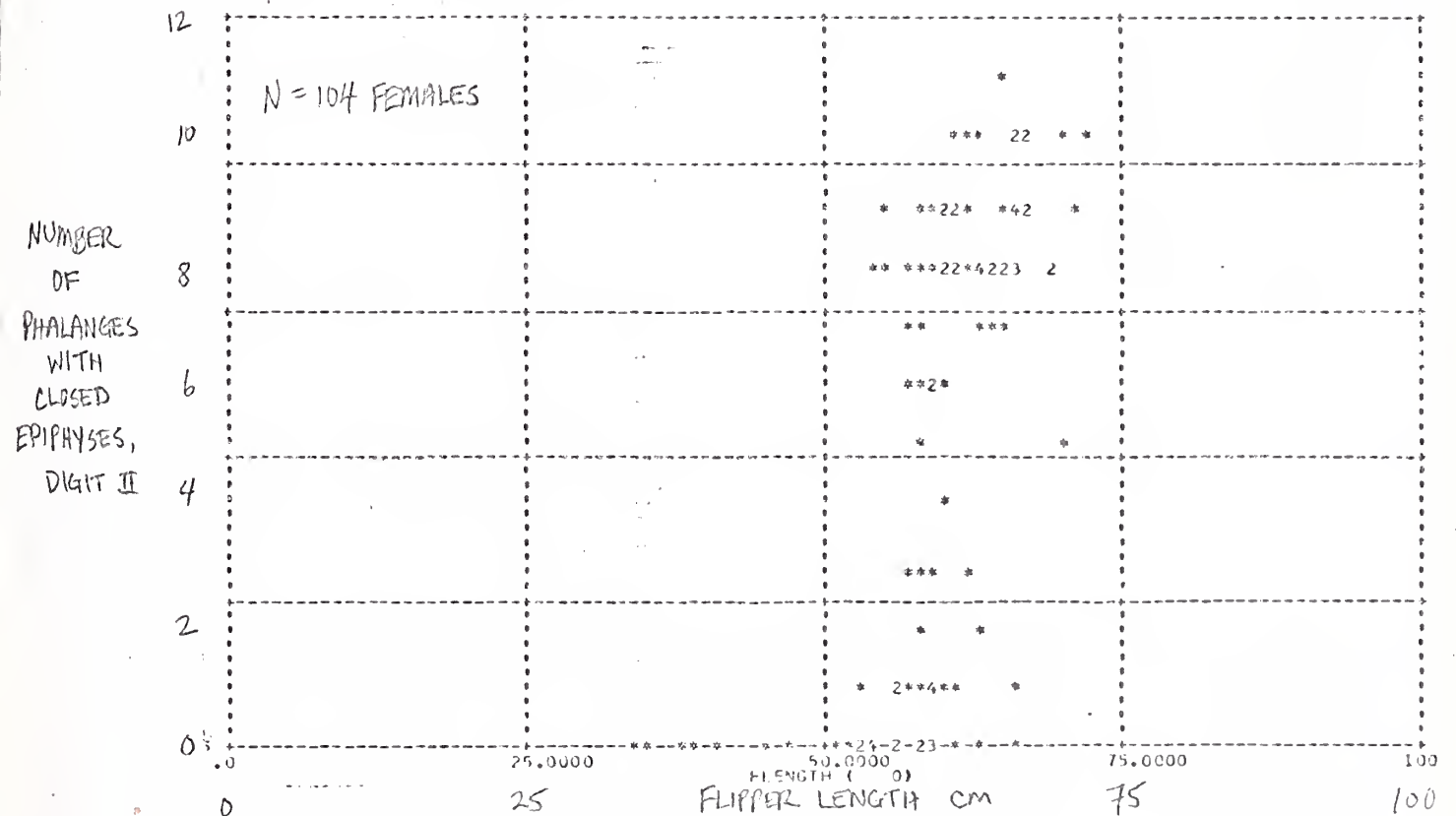
Graph 20: FEMALE NUMBER OF PHALANGES WITH CLOSED EPIPHYSES IN DIGIT II
VS FLIPPER LENGTH
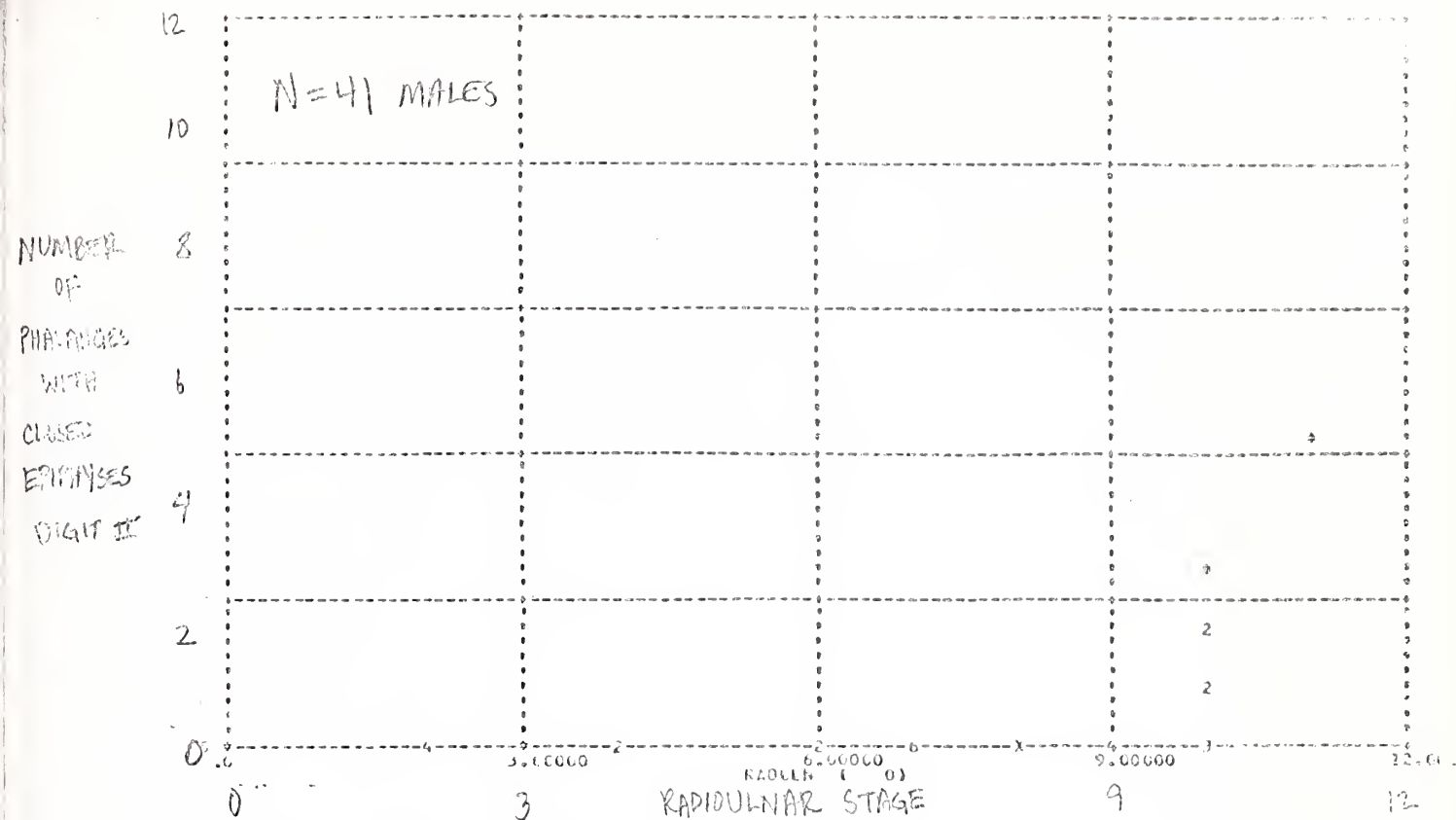
Graph 21: MALE NUMBER OF PHALANGES WITH CLOSED EPIPHYSES IN DIGIT II
VS RADIOULNAR STAGE
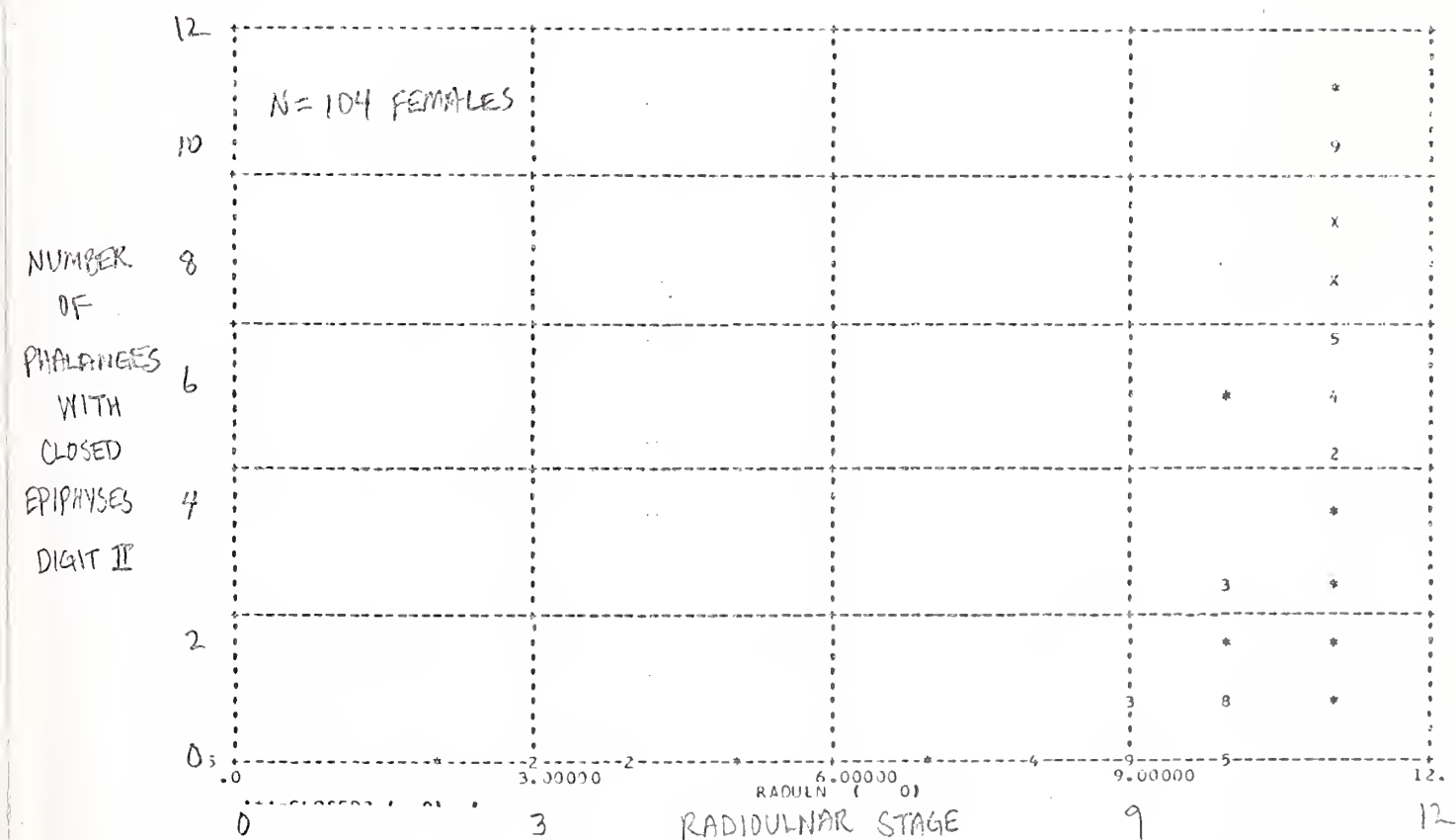
Graph 22: FEMALE NUMBER OF PHALANGES WITH CLOSED EPIPHYSES IN DIGIT II
VS RADIOULNAR STAGE

than an ankylosis from an arthritis, such as that in humans or that reported for the vertebrae of G. melena by Cowan (1966b).

The radiographic appearance of the ankylosing joint is illustrated by C-184 and C-150 (figure 10 and 11). The ankylosing joint appears first as a narrowing of the lucent joint space. This is followed by a slight but definite increase in density of the bone immediately subjacent to the articular cartilage, not unlike the subchondral sclerosis seen in human degenerative joint disease. These changes usually begin at one part of the joint surface instead of across the entire joint; in the humeral-ulnar joint, these changes start at the posterior portion of the joint and extend anteriorly.

The radiographic survey revealed that the most common sites of ankylosis in these samples were at the humeral-ulnar joint, the proximal radio-ulnar joint, the ulnar-ulnar carpal joint, and various carpal-carpal and carpal-metacarpal joints (table 7). Examples of humeral-radial, radial-carpal, and metacarpal-phalangeal joint fusions were also found.

Elucidation of the mechanism of these joint changes must await the histologic study.

Sexual Maturity, Physcial Maturity, and Flipper Maturity.

In order to investigate the relationship between flipper maturation, sexual maturity, and overall physical maturity, plots of flipper length, radioulnar stage, and the digital epiphyseal number were made against testis weights[7] for nine males; "sexual maturity"[8] for 32 females; and

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[7]Testes in cetaceans show a sharp increase in weight with the onset of sexual maturity; for this species, the immature testes weigh less than 200 gm, and the mature testes about 1 kg.

[8]Sexual maturity in the female is best judged by examination of the ovaries, uterus, and the mammae. The animals in this sample were categorized as mature, probably mature, or immature by JGM, and his data were used here.

TABLE 7

FREQUENT LOCATIONS OF SYNOSTOSES

|	Male	Female
Number of animals in sample	43	110
Humeral-ulnar joint synostosis	9	70
Proximal radio-ulnar	1	29
Ulnar carpal-5th metacarpal	2	18
Int. carpal - C3	1	16
Ulnar carpal-ulna	0	10
Int. carpal-C2	0	10
Ulnar carpal-C3	0	4

the status of the thoracic vertebral epiphyses[9] for both sexes.

Graphs 23 and 24 show that the increases in testis weights oc-curs at flipper lengths 75 to 85 cm, and at radioulnar stages 9-10; i.e., as the distal radial and ulnar physes begin to close. In graph 25 we see that only one of the four sexually mature males had fewer than six phalanges with epiphyses. These very limited data suggest that flip-per length and radioulnar stage may provide a means of predicting testis weights (and therefore sexual maturity) from an x-ray of the flipper; this would be a useful procedure for those maintaining cetaceans in cap-tivity, for breeding animals, or for studying herd structure. Hui (1975) found that in Delphinus delphis his "flipper index" correlated linearly reasonably well with testis weights; the radioulnar stage used in this report is conceptually similar to Hui's flipper index.

Graphs 26, 27, and 28 demonstrate that in females, sexual maturity does not occur with flipper length less than 50 cm., radioulnar stage less than 9, or with digital epiphyseal numbers less than 4 in this sample of 35 animals. However, once above these values, the flipper parameters cannot predict the sexual maturity of the female G. macrorhyncha. These results agree with those of Hui (1975), who found that neither the flip-per length nor his "flipper index" could predict sexual maturity in the female D. delphis.

Graphs 29 through 34 show the flipper parameters plotted against the state of the thoracic vertebral epiphyses for 10 males and 32 fe-males. The single male with fused vertebral epiphyses had a 93 cm. flip-per with a radioulnar stage 10 and a digital epiphyseal number of 8;
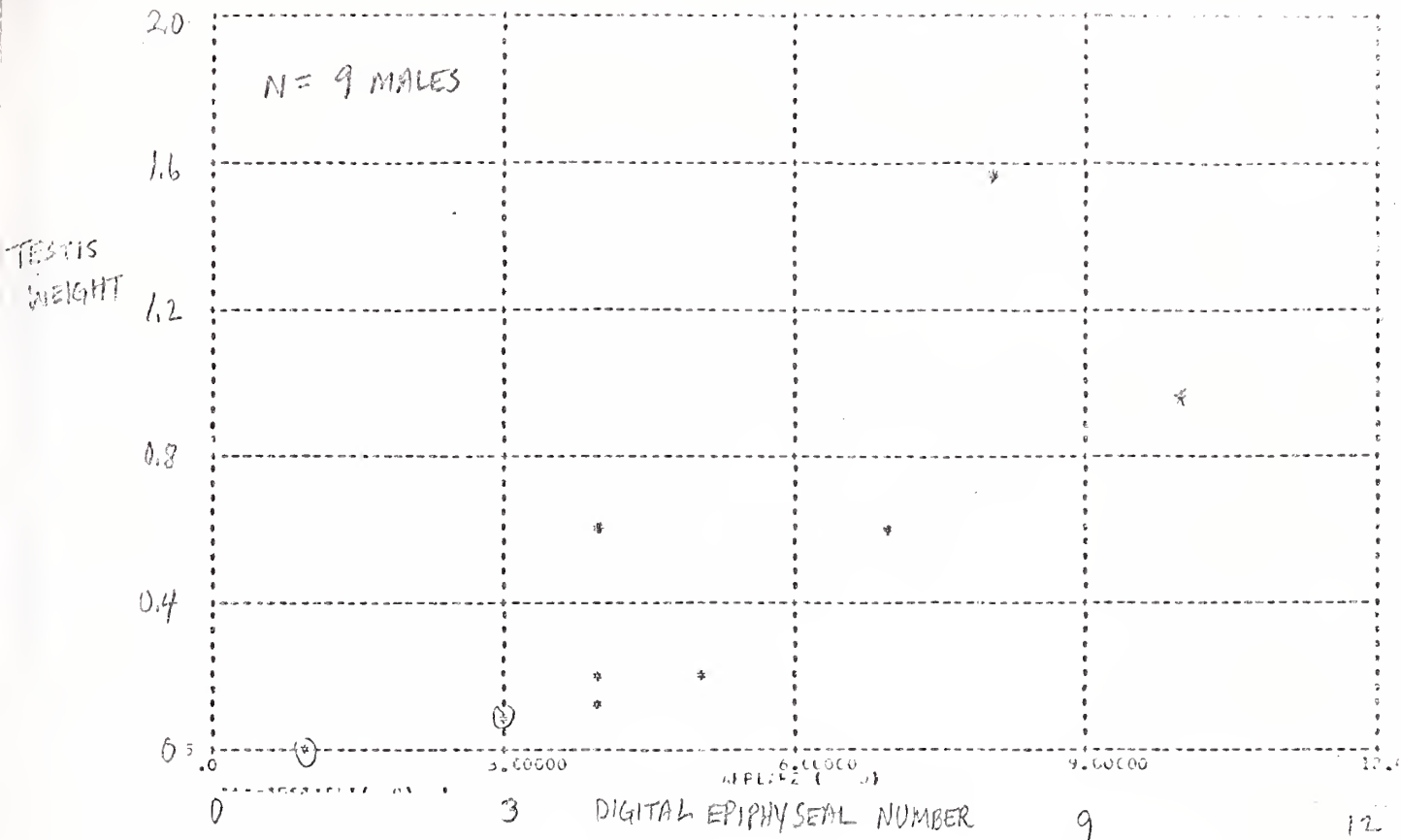
[9]Classified by JGM as open, closed but visible, or fused and invisible.
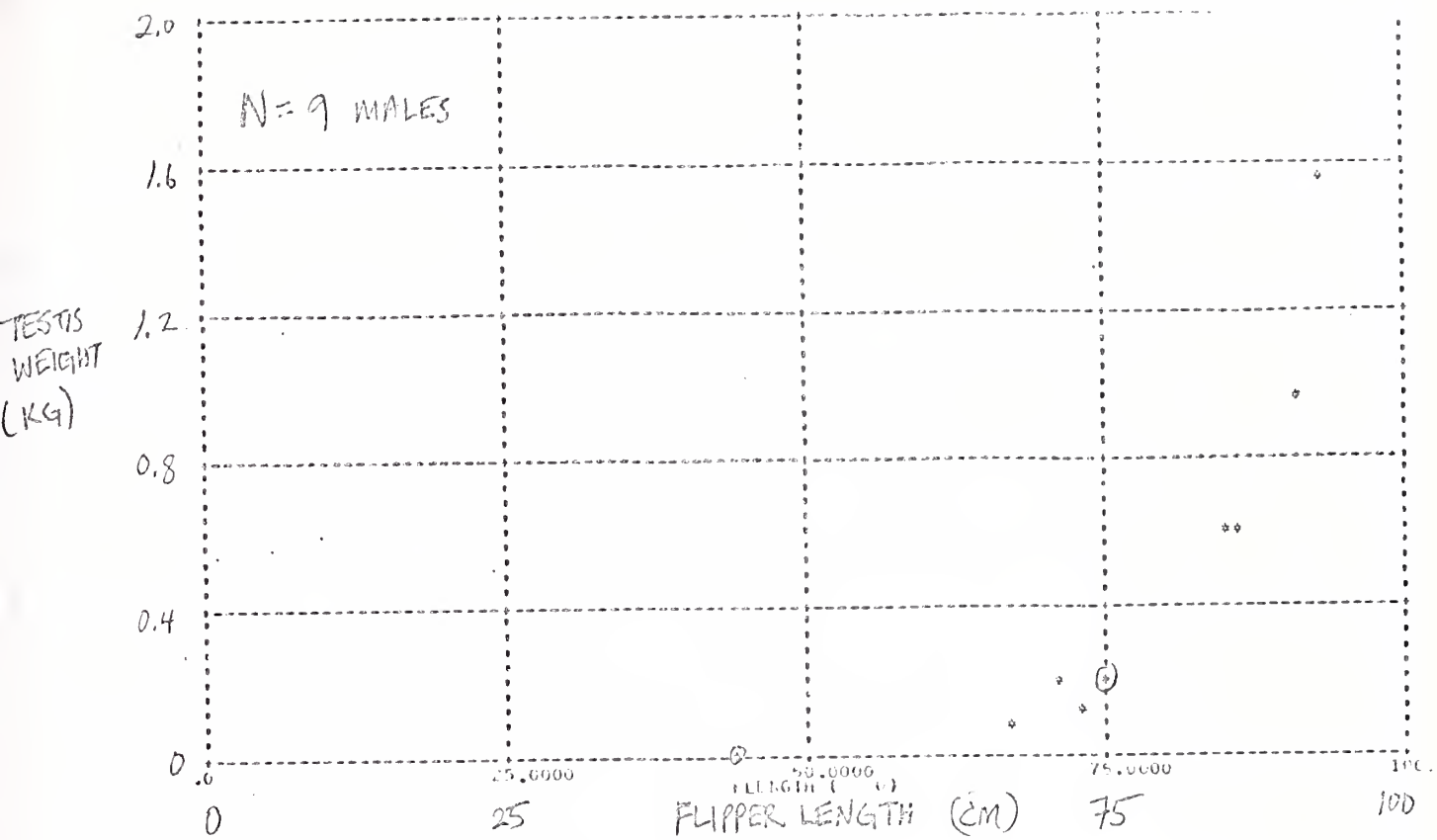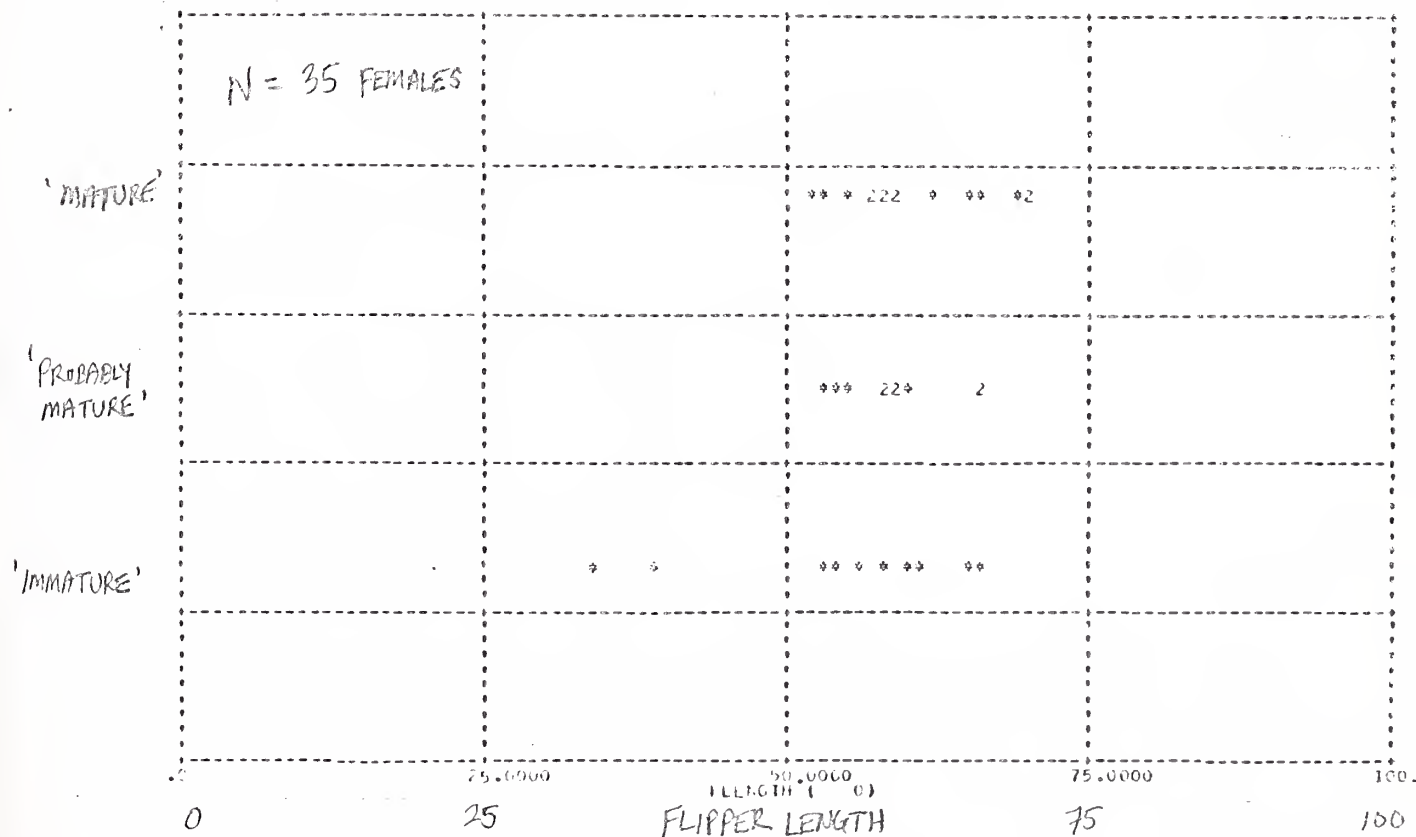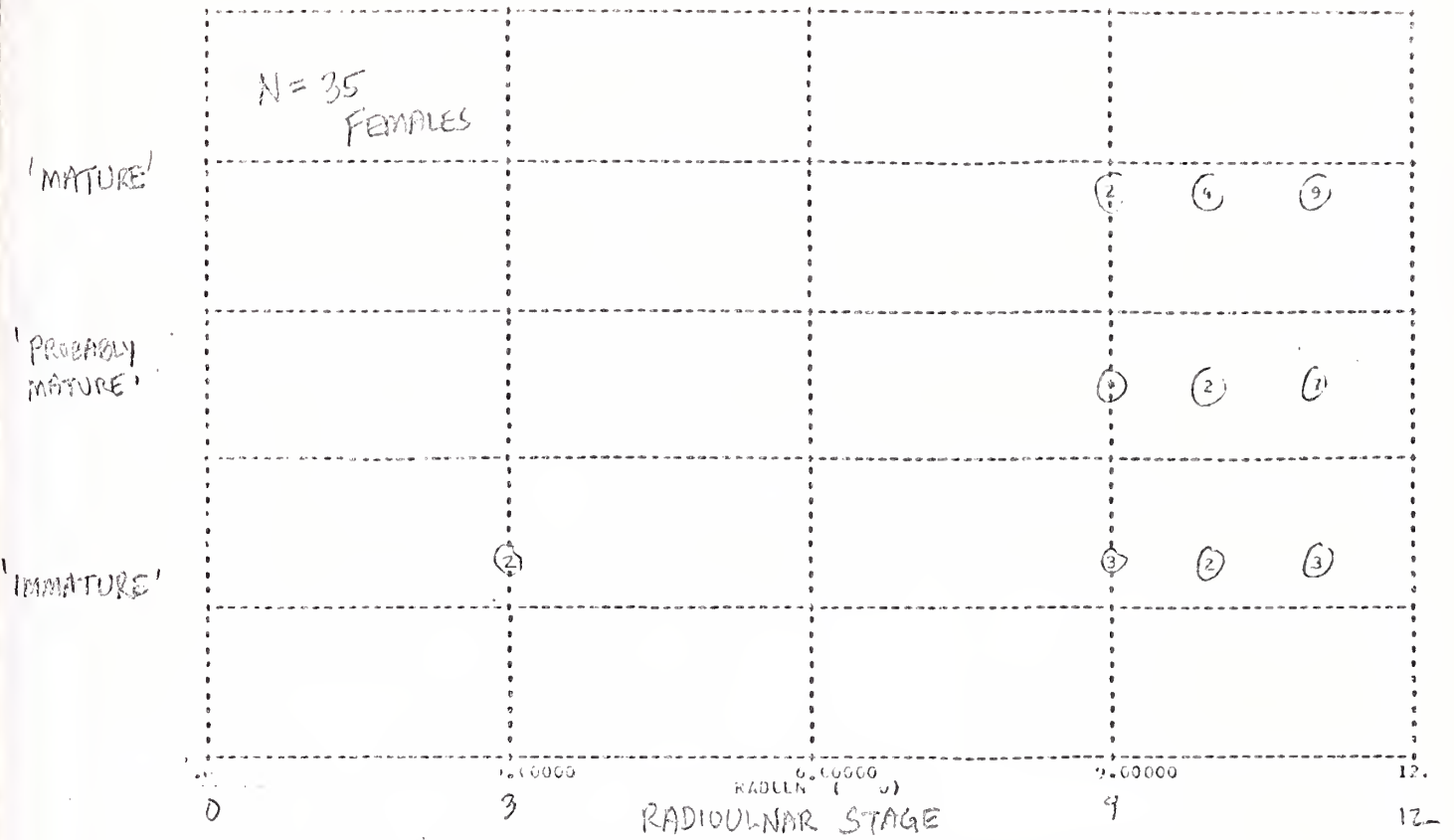
Graph 23: TESTIS WEIGHT VS FLIPPER LENGTH
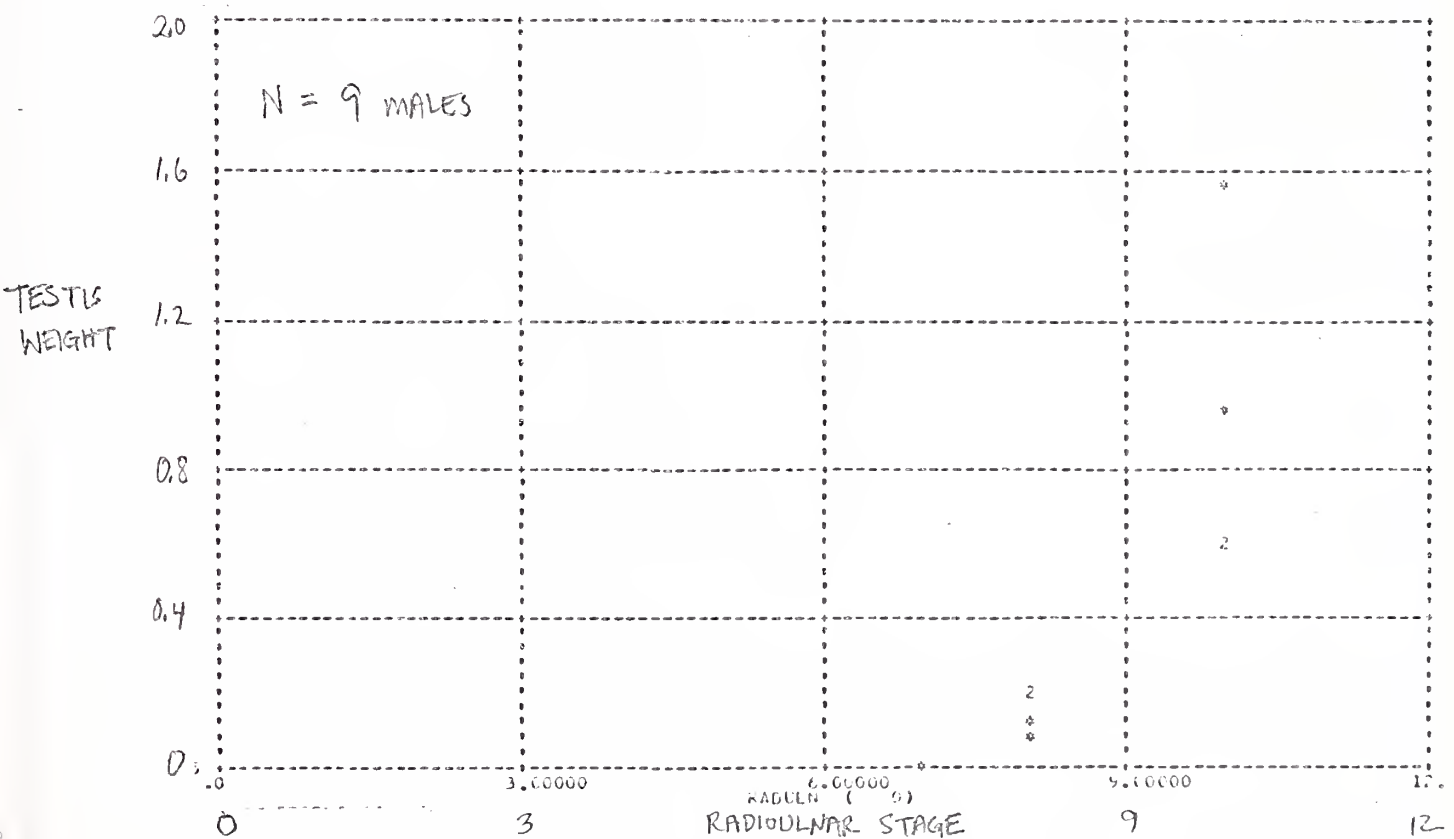
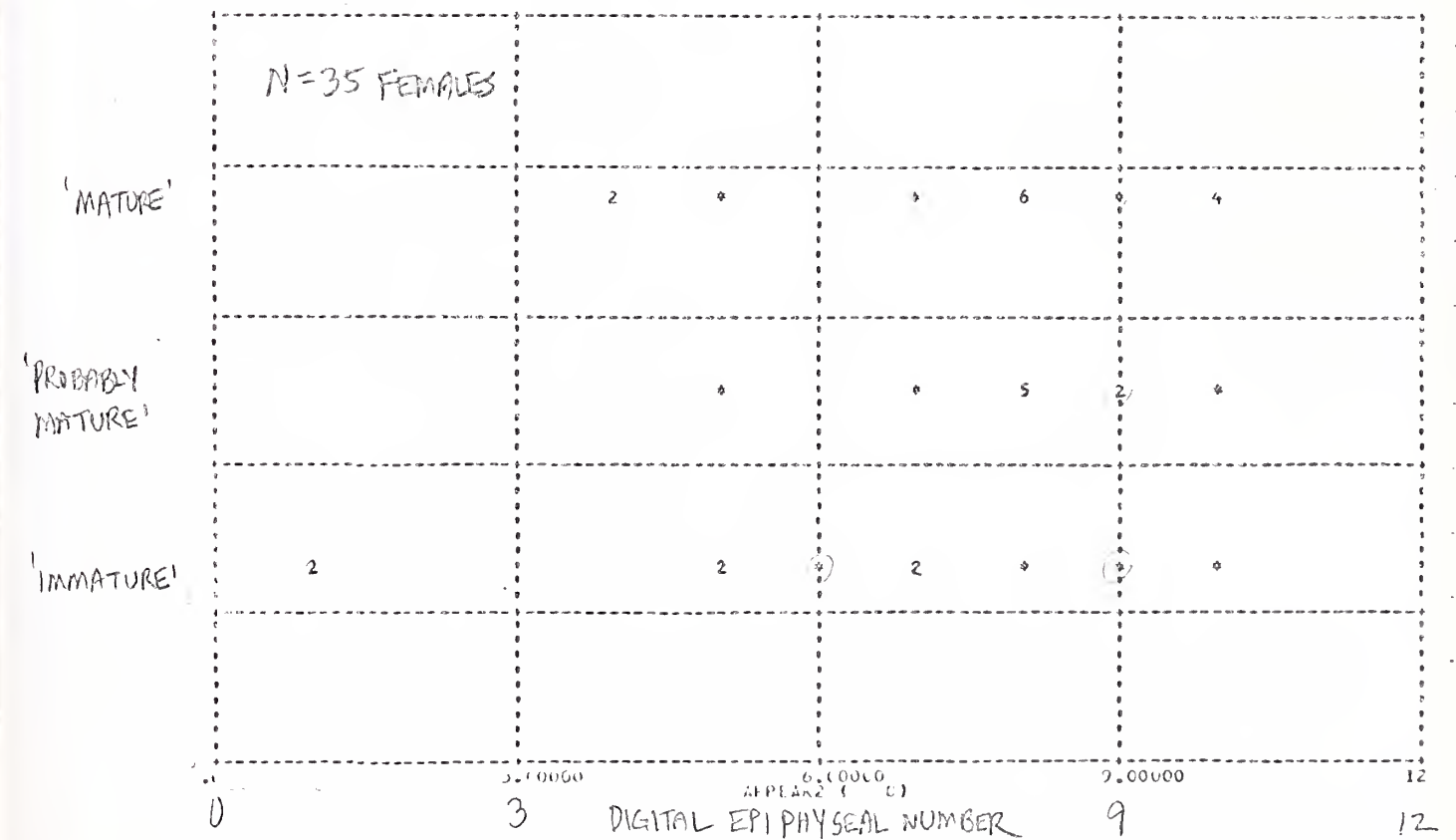Graph 24: TESTIS WEIGHT VS. RADIOULNAR STAGE
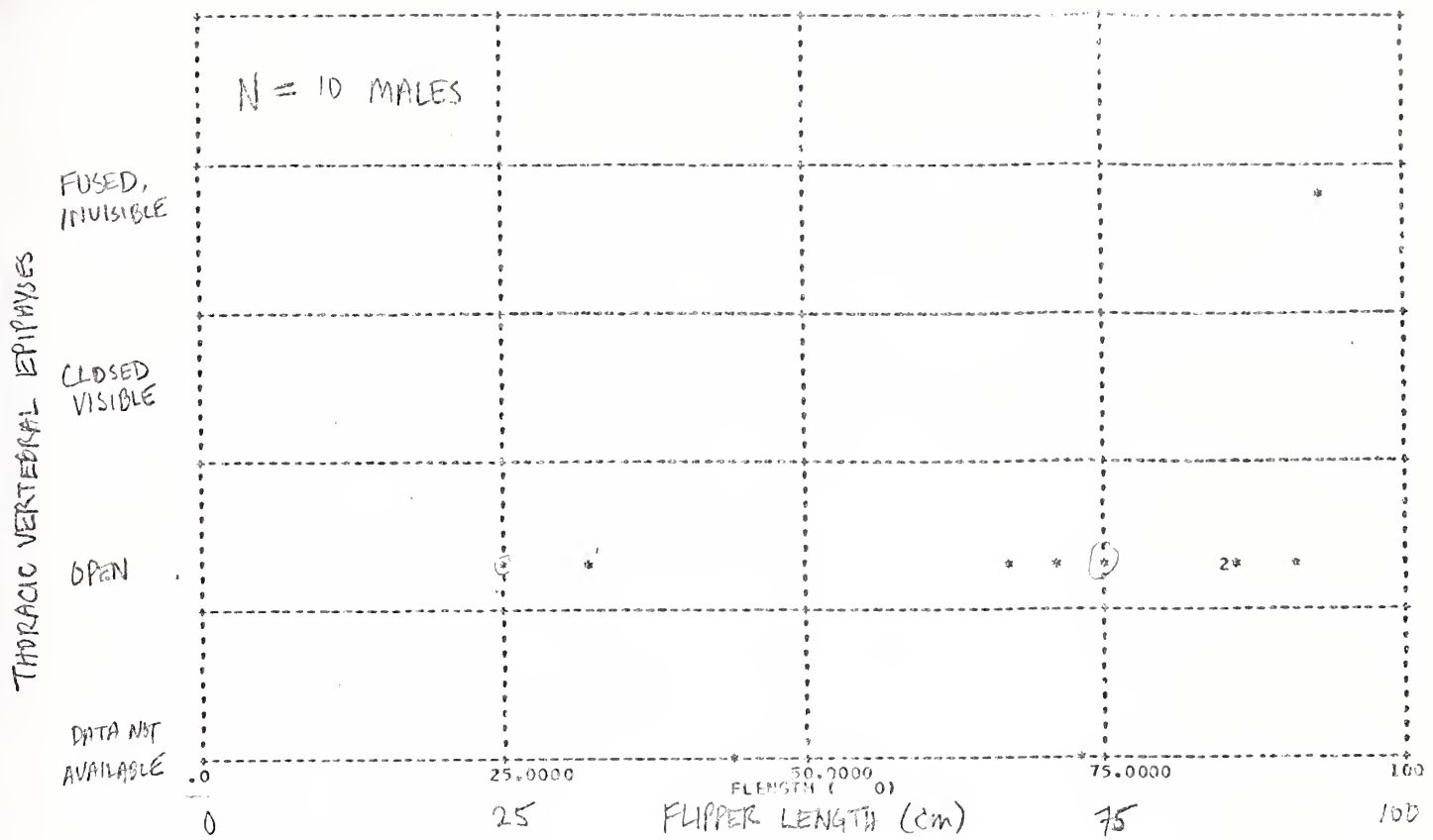
Graph 25: TESTIS WEIGHT VS DIGITAL EPIPHYSEAL NUMBER.
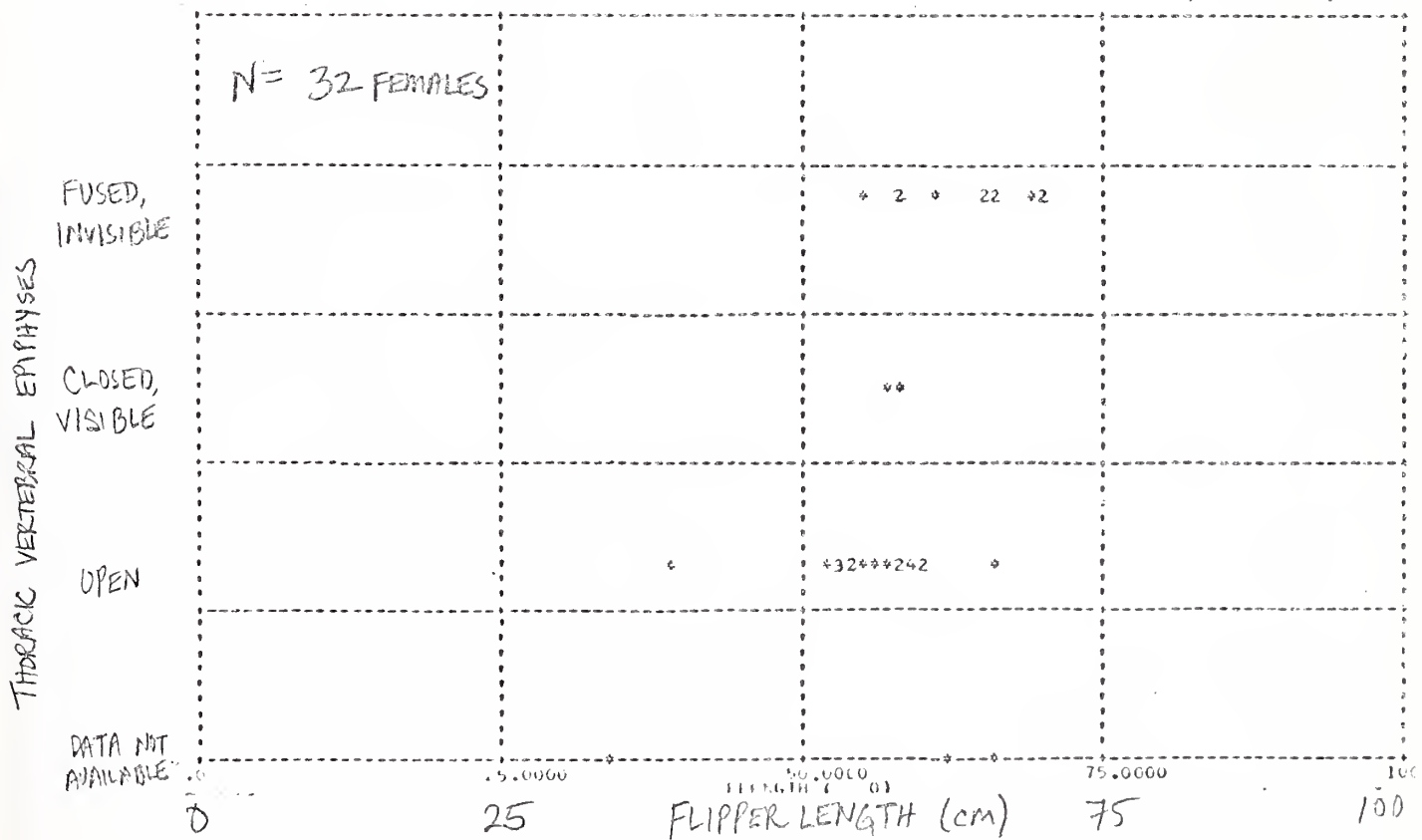

Graph 26: FEMALE SEXUAL MATURITY VS FLIPPER LENGTH

Graph 27: FEMALE SEXUAL MATURITY VS. RADIOULNAR STAGE

Graph 28: FEMALE SEXUAL MATURITY VS. DIGITAL EPIPHYSEAL NUMBER

Graph 29 : MALE THORACIC VERTEBRAL EPIPHYSEAL MATURITY VS FLIPPER LENGTH

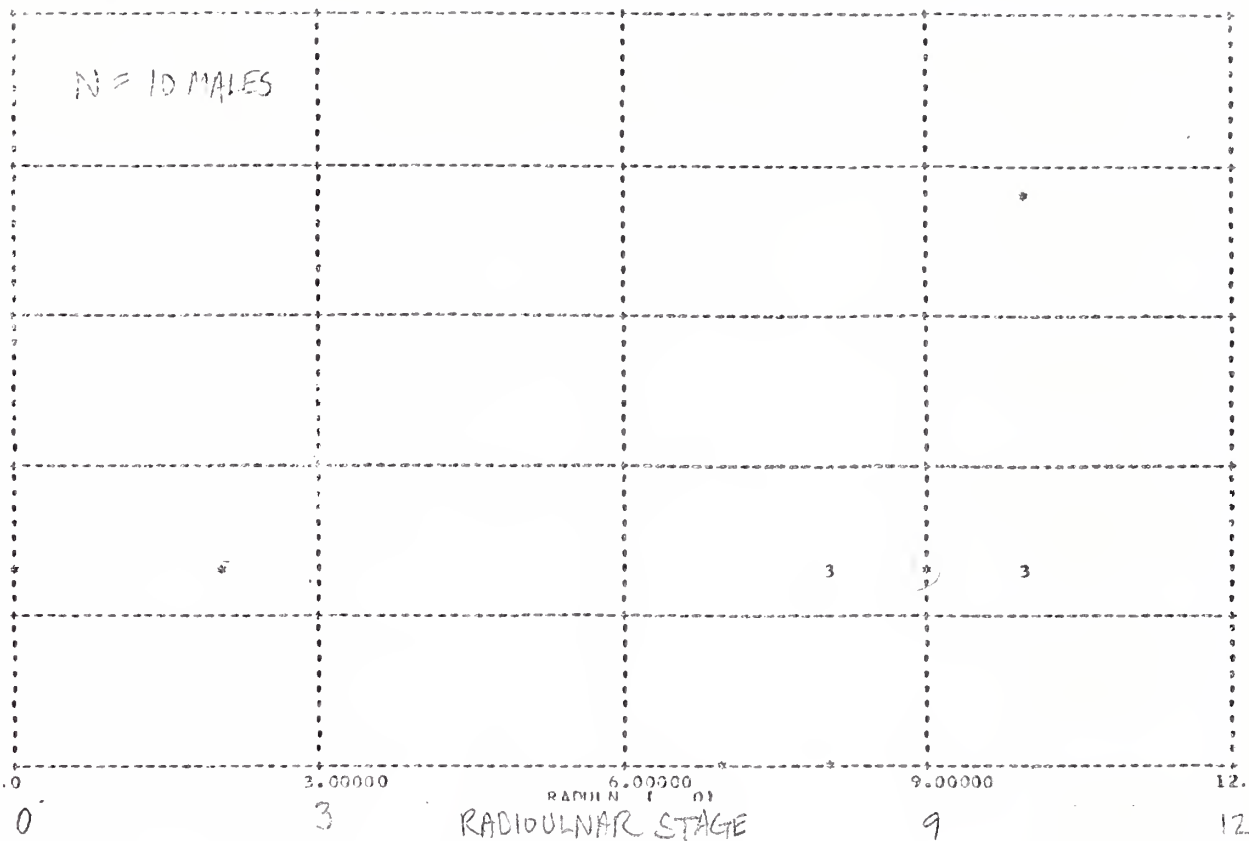Graph 30 : FEMALE THORACIC VERTEBRAL EPIPHYSEAL MATURITY VS.
FLIPPER LENGTH

Graph 31: MALE THORACIC VERTEBRAL EPIPHYSEAL MATURITY VS RADIOULNAR STAGE
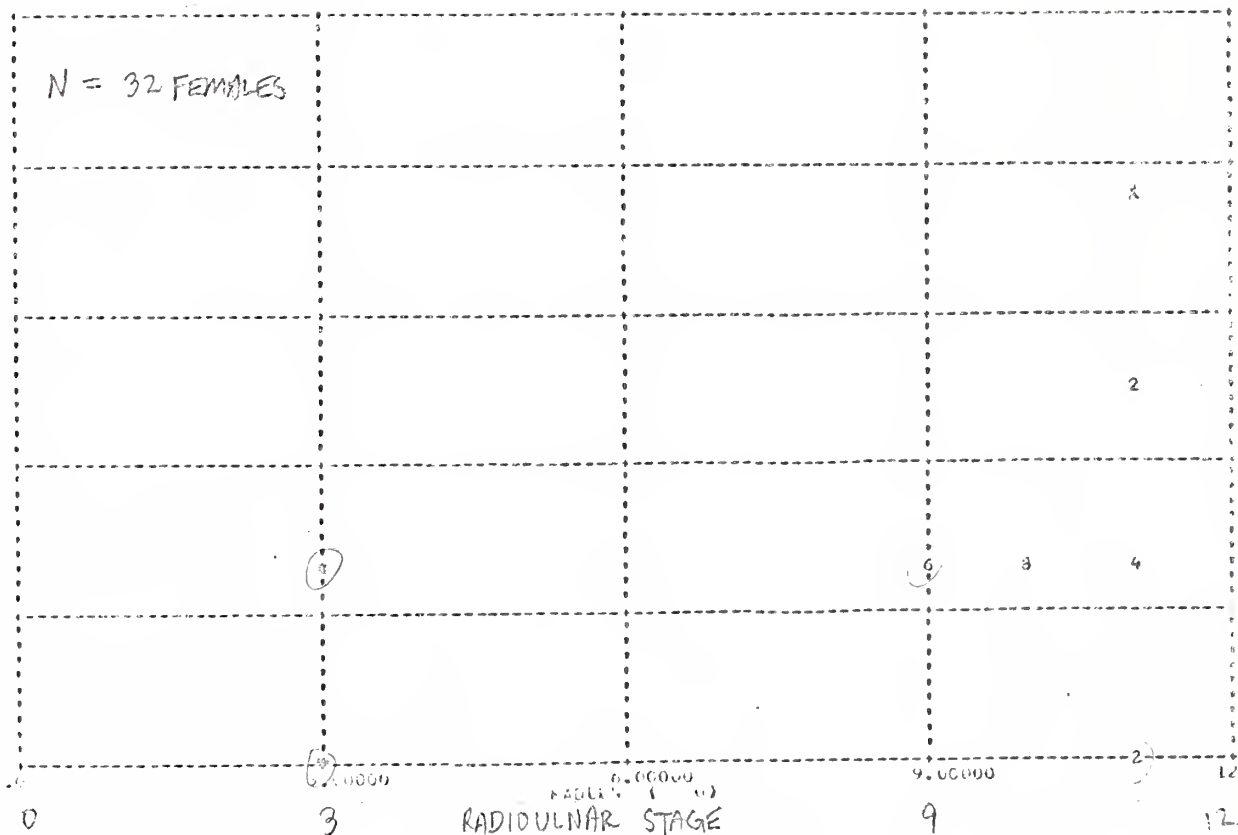
Graph 32: FEMALE THORACIC VERTEBRAL EPIPHYSEAL MATURITY VS RADIOULNAR STAGE
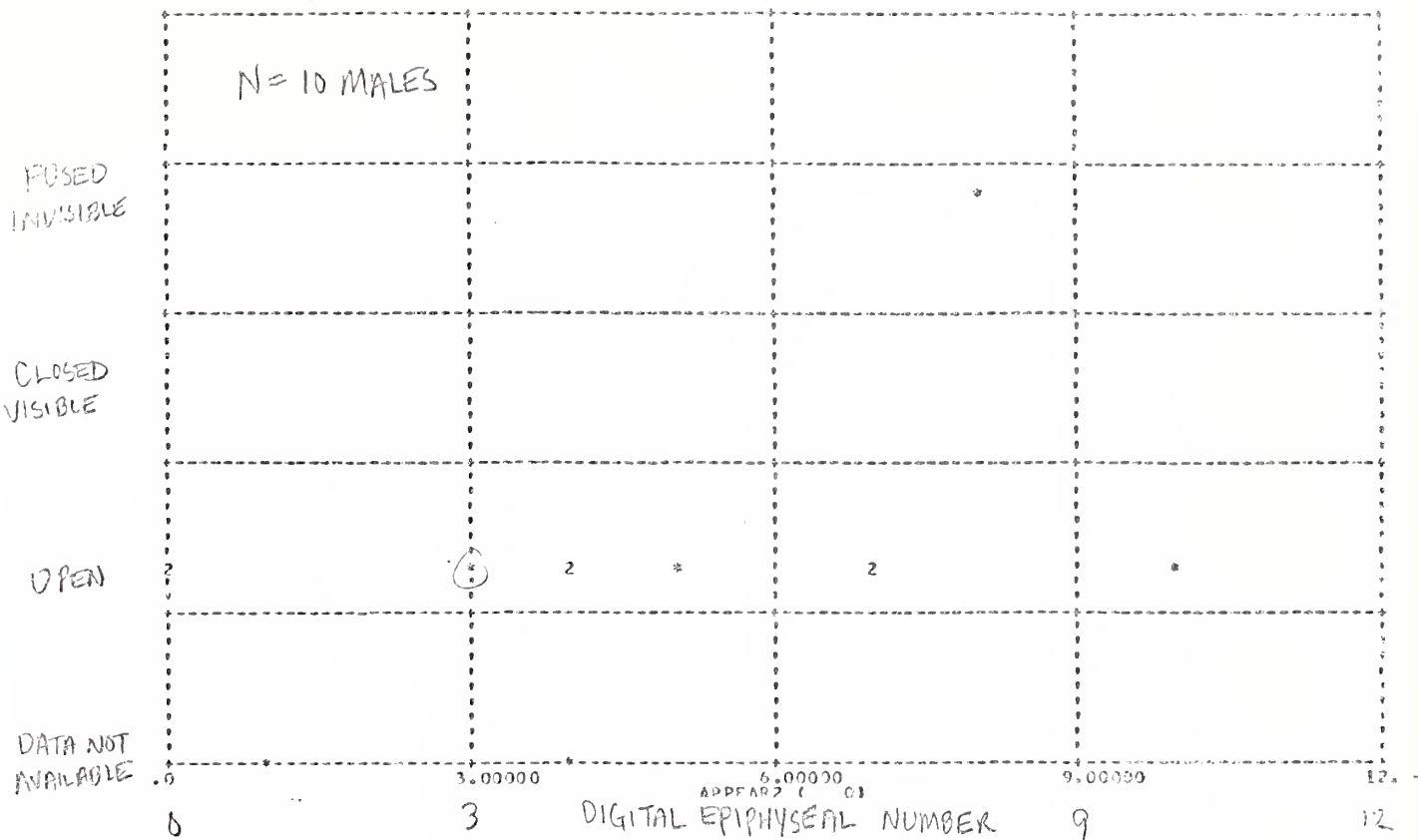
Graph 33 : MALE THORACIC VERTEBRAL EPIPHYSEAL MATURITY VS DIGITAL EPIPHYSEAL NUMBER
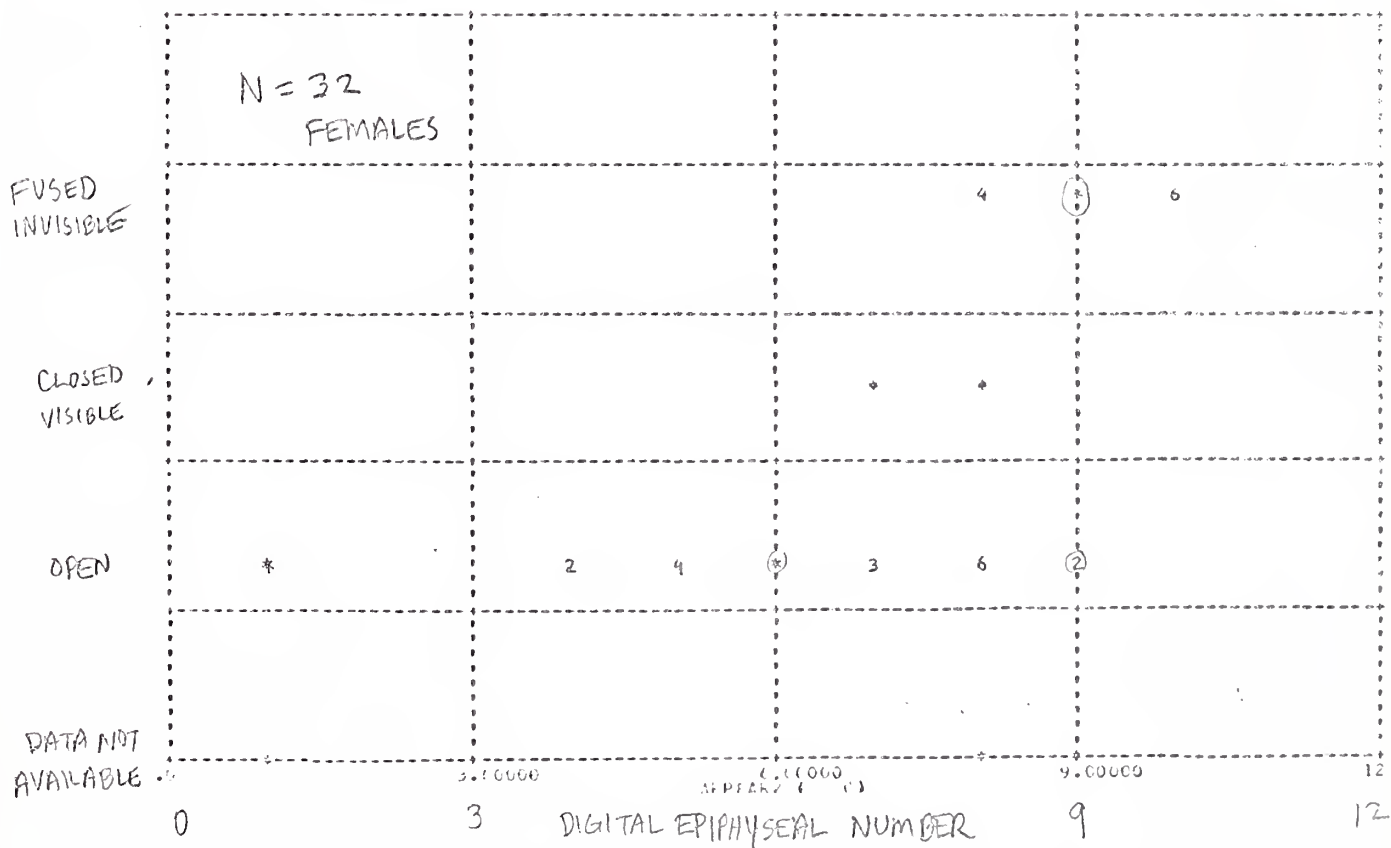
Graph 34 : FEMALE THORACIC VERTEBRAL EPIPHYSEAL MATURITY VS. DIGITAL EPIPHYSEAL NUMBER

however, the plots show immature males with values for each of the three parameters equal to or greater than those for the mature animal. These very limited data show, surprisingly, an apparent lack of correlation between vertebral physical maturity and flipper maturity; however, it must be emphasized that the data are extremely limited and the representation of vertebrally mature animals is quite inadequate.

Graph 32 shows that female flipper length does not predict vertebral maturity at any length greater than 50 cm. Graphs 33 and 34 indicate that no females with radioulnar stage less than 11 or digital epiphyseal number less than 8 had mature vertebrae. Again, none of the flipper parameters (except possibly for a digital epiphyseal nubmer of 10) appeared to reliably indicate vertebral maturity.

IV. DISCUSSION

As with any study in a relatively unexplored area, this study raises more questions than it answers. Points that have been clarified in this study on G. macrorhyncha that have not been adequately reported in the literature before include the following. Secondary ossification centers have been grossly and radiographically demonstrated in the cetacean carpal bones; these are not known to occur in any other animal. The number of phalanges in the flipper do not change with postnatal growth and maturation, in contrast to several previous conflicting reports. The joints in the flipper are neither "synchondroses" nor imperfect synovial joints, as previously reported, but rather fibrous joints. Digital epiphyses occur in adolescence and not only in the very largest animals. The vascular supply of the digital epiphyses appears to be primarily from transphyseal cartilage canals, even in well developed bony epiphyses; and the vascularization from the perichondrium, so important in the human, appears to have only a minor role in the whale. The proximal humeral, distal radial, and distal ulnar epiphyses each develop from multiple ossification centers. In addition, many findings previously published have been confirmed in this study.

The presence of epiphyses in the carpus is a quality unique to the cetaceans; no other species is known to have carpal epiphyses. The only similar structure which comes readily to mind is the apophysis of the human calcaneus. A comparative study of these two structures should be of great interest.

The patterns of vascularization of the digital epiphyses of the pilot whale merit some discussion. Cartilage canals are channels found in the chondroepiphysis which contain a muscular arteriole, a venule, loose connective tissue, and a variable number of capillaries and glomerular tufts. Cartilage canals are absent in the mouse and rat (Becks, et al 1948) but are present in larger mammals, such as the rabbit (Ring, 1955), the dog (Wilsman and Van Sickle, 1970, 1972), and man (Haraldson 1962, Gray and Gardner 1969, Gardner and Gray 1970, Ogden, 1974, 1977).

Recent textbooks of histology (Bloom and Fawcett 1968, Leeson and Leeson 1970) state that the chondroepiphysis remains avascular and that vascularization of the cartilage does not occur until after the onset of ossification in the avascular matrix. However, it is now clear that the chondroepiphysis already has a well-developed system of cartilage canals at birth, and that epiphyseal ossification begins immediately adjacent to the glomerular tufts within the cartilage canals (Wilsman and Van Sickle 1970, 1972, Gray and Gardner 1969, Ogden 1974, 1977). This latter finding is particularly significant in that it is strong evidence against the thesis that endochondral ossification may be triggered by a persistent lack of nutrition of the chondrocyte in an avascular matrix.

This radiographic and gross study demonstrates not only the existence of cartilage canals in the cetacean, but also that this vascular supply comes primarily from the diaphyseal-metaphyseal circulation by traversing the growth plate, and not from the perichondrium. In previous studies on smaller species, the cartilage canals and their

arterioles were found to originate almost exclusively from the peri-
chondrium, with either no (Wilsman and Van Sickle 1970, 1972, Harald-
son 1962) or only a few (Gray and Gardner 1969, Gardner and Gray 1970,
Ogden 1974, 1977) vessels traversing the growth plate and anastomosing
with the metaphyseal circulation. Thus, the pattern of vasculariza-
tion of the cetacean epiphysis is uniquely different from that of
smaller mammals. Whether this relative lack of vascularization from
the perichondrium is related to the sheer physical size of the species,
or to the relatively avascular nature of the surrounding soft tissue,
or to other factors, is unclear. Histologic and angiographic studies
of the cetacean epiphyses and studies on other large mammals would
help clarify this question.

Another attribute of the unexplored area is that there is al-
ways fertile ground for speculation. It is well known that mechanical
stresses on bone tissue affect the rate of osteogenesis both in vitro
(Bassett 1964, Hall 1970) and in vivo (Meikle 1973) in animal models.
The effect of mechanical stresses on bone growth in the form of frac-
ture healing is the subject of much current orthopaedic research.
It is tempting to speculate that the slowness of ossification, parti-
cularly of the secondary centers and the phalanges, in the cetacean may
be due in part to its aquatic environment and the lack of terrestial
weight-bearing stresses.

While there are no reports of measurements of oxygen tension
within the cetacean flipper, the circulatory changes of the diving
reflex must result in considerable periods of decreased blood flow and
hypoxia in the flipper. Low oxygen tension not only predisposes to
chondrogenesis and fibrous tissue formation in bone tissue culture

(Bassett 1964, Hall 1970) but also suppresses bone resorption in tissue culture (Goldhaber 1963). One cannot help but wonder if hypoxia contributes to the slow ossification and the very slow remodelling in cetacean bone.

The slow appearance of postnatal ossification centers and slow remodelling are similar to the skeletal changes observed in human hypothyroidism. The tendency of secondary centers to develop from multiple small centers of ossification within the chondroepiphysis is especially reminiscent of the changes of epiphyseal dysgenesis of the femoral heads seen in cretinism (Jaffe, 1975). Fawcett (1942) demonstrated evidence for hypothyroidism in the Florida manatee, which also had amedullary bones. The same is yet to be seen for cetaceans.

The prevalance of synostoses in mature animals implies that ankylosis of the joints is part of the natural history of the flipper, rather than part of a pathologic process. Cowan's (1966b) attribution of the ankylosis of vertebrae to degenerative disease or osteoarthritis is quite unlikely; osteoarthritis in humans does not result in ankylosis. More likely the reported vertebral fusions and possibly the "congenital block vertebrae" Cowan also reported are both the result of a similar or identical process to that in the flipper.

The pattern and history of progressive ankylosis of the joints of the maturing flipper is more reminiscent of the progressive synostoses of the hands and forearm seen in Apert's syndrome (Cohen 1975, Hoover et al 1970, Schauerte and St. Augin 1966), than of rheumatoid disease. The lack of synovium, the maintainance of the normal cetacean joint, and the erosion of the joint cartilage from within the bone argue against

a rheumatoid-type process. The frequency of ankylosis occuring at the humeral-ulnar joint and in the more ulnarly located inter-carpal joint suggests that mechanical pressure may be a factor in ankylosis, since these joints would bear the compressive load resulting from the force of water resistance on the flipper of the swimming cetacean.

There is much work which should be done. The careful histologic examination of ossification in the cetacean primary and secondary centers, the carpal secondary centers, the digital epiphyses and their vasculature, and the ankylosing joint all should prove to be of great interest. Fetal specimens would be indispensible in investigating the prenatal patterns of development. Angiographic studies should be helpful in clarifying the vascular supply of the flipper and of the epiphyses. The relationships of flipper maturity, age, sexual maturity, and vertebral physical maturity remained muddled. And perhaps someday the bones of the cetacean flipper will be useful in the development of a sophisticated mathematical model of bone growth.

BIBLIOGRAPHY

1. Basset, C.A.L: Environmental and Cellular Factors Regulating Osteogenesis, in Bone Biodynamics, Frost, H.M. (ed.), Little Brown and Co., Boston, pp. 233-244, 1964.

2. Becks, H., Asling, C., Simons, M., Evans, H., Li, C.: Ossification at the Distal End of the Humerus in the Female Rat. Amer. J. Anat., 82, 203-229, 1948.

3. Bloom, W., and Fawcett, D.W.: A Textbook of Histology, 9th Ed., W. B. Saunders Co., Philadelphia, 1968.

4. Brown, D.H.: Behavior of a Captive Pilot Whale. J. Mammal. 41, 342, 1960

5. Cohen, M.M: An Ideologic and Nosologic Overview of the Carniosynostosis Syndromes. Birth Defects O.A.S., 11(2), 137-189, 1975.

6. Cope, E.D.: Fourth Contribution to the History of Existing Cetacea. Proc. Acad. Nat. Sci., Philadelphia pp. 129-139, 1876.

7. Cowan, D.F.: Observations on the Pilot Whale G. melena, Organ Weight and Growth. Anat. Record, 155, 623-628, 1966a.

8. Cowan, D.F.: Pathology of the Pilot Whale. Arch. Path. 82, 178-189, 1966b.

9. Fawcett, D.W.: The Amedullary Bones of the Florida Manatee. Am. J. Anat. 71, 271-309, 1942.

10. Felts, W.J.L.: Some Functional and Structural Characteristics of Cetacean Flippers and Flukes. In Whales, Dolphins, and Porpoises, Norris, K.S. (ed.), Univ. of Calif. Press, Berkeley, pp. 255-276, 1966.

11. Felts, W.J.L., and Spurell, F.A.: Structural Orientation and Density in Cetacean Humeri. Am. J. Anat. 116, 171-204, 1965.

12. Felts, W.J.L., and Spurell, F.A.: Some Structural and Developmental Characteristics of Cetacean Radii: A Study in Adaptive Osteogenesis. Am. J. Anat. 118, 103-134, 1966.

13. Flower, W.H.: _An Introduction to the Osteology of the Mammalia._ McMillan and Co., London, 1876.

14. Frazer, J.F.D., and Huggett, A. St.G.: The Growth Rate of Foetal Whales. J. Physiol. _146_, 21P-22P, 1959.

15. Gardner, E., and Gray, D.: The Prenatal Development of the Human Femur. Am. J. Anat. _129_, 121-140, 1970.

16. Gaskin, D.E.: _Whales, Dolphins, and Seals_, Heinemann Educational Books, Ltd., London, 1972.

17 Goldhaber, P.: Some Chemical Factors Influencing Bone Resorption in Tissue Culture. Publ. Am. Assoc. Adv. Sci. _75_, 609-636, 1963.

18. Gray, D.J., and Gardner, E.: Prenatal Development of the Human Humerus. Am. J. Anat. _124_, 431-466, 1969.

19. Gunther, G.: Records of the Pilot Whale or Blackfish from the Texas Coast. J. Mammal. _27_, 374-377, 1946.

20. Haines, R.W.: The Histology of Epiphyseal Union in Mammals. J. Anat. _120_, 1-25, 1975.

21. Hall, B.K.: Cellular Differentiation of Skeletal Tissue. Biol. Rev. Camb. Phil. Soc. _45_, 455-484, 1970.

22. Haraldson, S.: The Vascular Pattern of a Growing and a Full-Grown Epiphysis. Acta Anat. _48_, 156-167, 1962.

23. Harrison, R.J., and King, J.E.: _Marine Mammals_, Hutchinson University Library, London, 1965.

24. Hoover, G.H., Flatt, A.E., and Weiss, M.W.: The Hand and Apert's Syndrome. J. Bone and Joint Surg. _52A_,878, 1970.

25. Howell, A.B.: _Aquatic Mammals_. Charles C. Thomas, Springfield, Illinois 1930a.

26. Howell, A.B.: Myology of the Narwhale (_Monodon monoceros_). Am. J. Anat. _46_, 187-215, 1930b.

27. Huggett, A. St. G., and Widders, W.F.: The Relationship Between Mammalian Foetal Weight and Conception Age. J. Physiol. _114_, 306-317, 1951.

28. Hui, C.A.: Growth and Physical Indices of Maturity, presented at the Dolphin Breeding Workshop, San Diego, Calif., draft from the Biomedical Division, Code 402, Naval Undersea Center, San Diego, Calif., 1975.

29. Hui, C.A.: Reliability of Using Dentin Layers for Age Deter-
     mination in _Tursiops truncatus_. A Report to the Marine Mam-
     mal Commision, MMC-155, 1977.

30. Jaffe, H.L.: Metabolic, Degenerative, and Inflammatory Dis-
     eases of Bones and Joints, Lea and Feibiger, Philadelphia,
     1975.

31. Krebs, H.A.: The August Krogh Principle: "For many Problems
     There is an Animal on Which it Can Be Most Conveniently Studied".
     J. Exp. Zool. 194, 221-226, 1975.

32. Kritzler, H.: Observations on the Pilot Whale in Captivity.
     J. Mammal.33, 321-334, 1952.

33. Kükenthal, W.: Über die Hand der cetacean. Anat. Anz. 3,
     638-646, 1888a.

34. Kükenthal, W.: Über die Hand der Cetacean (Zweite Mitteilung).
     Anat. Anz. 3, 912-916, 1888b.

35. Kükenthal, W.: Über die Hand der Cetacean (Dritte Mitteilung).
     Anat. Anz. 5, 44-52, 1890a.

36. Kükenthal, W.: Cetologische Notiz. Anat. Anz. 5, 709-710,
     1890b.

37. Kunze, A.: Über die Brustflosse der Wale. Zool. Jahrb. Anat.
     Abteil. 32, 575-651, 1912.

38. Leboucq, H.: Recherches sur la Morphologie de la Main chez les
     Mammiferes Marins. Archiv. Biol. 9, 571-648.

39. Leeson, T.S., and Leeson, C.R.: _Histology_. W. B. Saunders Co.,
     Philadelphia, 1970.

40. McMahon, T.: Size and Shape in Biology. Science 179, 1201-
     1204, 1973.

41. Meikle, M.C.: _In Vivo_ Transplantation of the Mandibular Joint
     of the Rat; an Autoradiographic Investigation into Cellular
     Changes at the Condyle. Arch. Oral Biol. 18, 1011-1020, 1973.

42. Meikle, M.C.: The Influence of Function on Chondrogenesis at
     the Epiphyseal Cartilage of a Growing Long Bone. Anat. Record
     182, 387-400, 1975.

43. Meister, W.: Histologic Structure of the Long Bones of Penguins.
     Anat. Record 143, 377-387, 1962.

44. Needler, A.W.H.: Blackfish (Globicephalus) Stranded on the South Coast of Prince Edward Island. Can. Field Nat. 45, 157-158, 1931.

45. Nishiwaki, M. and Kasuga, T.: Osteological Note of an Antartic Sei Whale. Sci. Rep. Whales Res. Inst. (Tokyo) 23 83-89, 1971.

46. Norris, K.S.: Standardized Methods for Measuring and Recording Data on the Smaller Cetaceans. J. Mammal. 42, 471-476, 1961.

47. Ogden, J.A.: Anatomic and Histologic Study of Factors Affecting Development and Evolution of Avascular Necrosis in Congenital Hip Dislocation. In The Hip: Proceedings of the Second Open Scientific Meeting of the Hip Society, 1974, Harris, W.H. (ed.), Mosby Co., St. Louis, pp. 125-153, 1974.

48. Ogden, J.A.: The Development and Growth of the Musculoskeletal System. in Basic Science in Orthopaedics, Albright, J.A. and Brand, R., eds., Appleton-Century-Crofts, New York, in preparation (1977).

49. Ohe, T.: Distribution of the Red Marrow in the Bones of the Fin Whale. Sci. Rep. Whales Res. Inst. (Tokyo) 3, 17-22, 1950.

50. Omura, H., Ichihara, T., Kasuya, T.: Osteology of the Pygmy Blue Whale with Additional Information on External and Other Characteristics. Sci. Rep. Whales Res. Inst. (Toyko) 22, 1-28, 1970.

51. Omura, H.: A Comparison of the Size of Vertebrae Among Some Species of the Baleen Whales with Special Reference to Whale Movements. Sci Rep. Whales Res. Inst. (Tokyo) 23, 61-69, 1971a.

52. Omura, H., Nishiwaki, M., Kasuya, T.: Further Studies on Two Skeletons of the Blick Right Whale in the North Pacific. Sci. Rep. Whales Res. Inst. (Tokyo) 23, 71-81, 1971b.

53. Omura, H.: An Osteological Study of the Cuvier's Beaked Whale, Ziphius Cavirostris in the Northwest Pacific. Sci. Rep. Whales Res. Inst. (Tokyo) 24, 1-34, 1972.

54. Paradiso, J.L.: The Common Blackfish in Virginia Coastal Waters. J. Mammal. 39, 440-441, 1958.

55. Park, E.A. and Powers, G.F.: Acrocephalosyndactylism. Am. J. Dis. Child. 20, 235-315, 1920.

56. Parry, D.A.: The Structure of Whale Blubber and its Thermal Properties. Quart. J. Microscop. Sci. 90, 13-26, 1949.

57. Ridgway, S.H. (ed.): Mammals of the Sea: Biology and Medicine. Chas. C. Thomas, Springfield, Illinois 1972.

58. Ring. P.A.: Ossification and Growth of the Distal Ulnar Epiphysis of The Rabbit. J. Anat. 89, 457-463, 1955.

59. Ryder, J.A.: On the Probable Origin, Homologies, and Development of the Flukes of Cetaceans and Sirenians. Am. Naturalist 19, 515-519, 1885a.

60. Ryder, J.A.: On the Genesis of the Extra Terminal Phalanges in the Cetacea. Am. Naturalist 19, 1013-1015, 1885b.

61. Ryder J.A.: On the Development of the Cetacea. U.S. Commision on Fish and Fisheries Report for 1885, pp.427-488, 1885c.

62. Schauerte, E.W. and St. Aubin, P.M.: Progressive Synostosis in Apert's Syndrome. Amer. J. Roent. 97, 67-74, 1966.

63. Scholander, P.F. and Schevill, W.E.: Countercurrent Vascular Heat Exchange in the Fins of Whales. J. Appl. Physiol. 8, 279-282, 1955.

64. Sergeant, D.E.: Age Determination in Odontocete Whales from Dentinal Growth Layers. Norwegian Whaling Gazette for 1959, 6, 273-288, 1959.

65. Sergeant, D.E.: The Biology of the Pilot or Pothead Whale Globicephala melena (Traill) in Newfoundland Waters. Bulletin of the Fisheries Res. Board of Canada No. 132, 1962a.

66. Sergeant, D.E.: On the External Characters of the Blackfish or Pilot Whale (genus Globicephala). J. Mammal. 43, 395-413, 1962b.

67. Slijper, E.J.: Whales, Basic Books, New York, 1962.

68. Starrett, A. and Starrett, P.: Observations of Young Blackfish Globicephala. J. Mammal. 36, 424-429, 1955.

69. Streeter, G.L.: Developmental Horizons in Human Embryos (Fourth Issue). A Review of Histogenesis of Cartilage and Bone. Contr. Embryol. Carnegie Inst. 33, 149-168, 1949.

70. Struthers, J.: On Some Points in the Anatomy of a Great Fin-Whale (Balenoptera musculus). J. Anat. Physiol. 5, 107-125, 1871.

71. Struthers, J.: Account of Rudimentary Finger Muscles Found in the Greenland Right Whale. J. Anat. Physiol. 12, 217-224, 1977.

72. Thompson, D.W.: On Growth and Form, abrg. ed., Bonner, J.T. ed. Cambridge Univ. Press, London, 1961.

73. Turner, W.: A Contribution to the Anatomy of the Pilot Whale (Globicephala Svineval, Lacipede). J. Anat. Physiol. 2, 66-79, 1868.

74. Vladykow, V.D.; A Modification of the Pectoral Fins in the Beluga from the St. Lawrence River. Naturaliste Canadien 70, 23-40, 1943.

75. Weber, M.: Anatomisches über Cetacean. Morphol. Jahrb. 13, 616-653, 1888.

76. Wilsman, N.J., and Van Sickle, D.C.: The Relationship of Cartilage Canals to the Initial Osteogenesis of Secondary Centers of Ossification. Anat. Record 168, 381-392, 1970.

77. Wilsman, N.J., and Van Sickle, D.C.: Cartilage Canals, Their Morphology and Distribution. Anat. Record 173, 79-94, 1972.

Figure 1: Specimen C-188, a 60.5 cm flipper from a
367 cm, 630 kg male <u>G. macrorhyncha</u>.
Dorsal surface of left flipper.

C-188

FIGURE 36. Left pectoral limbs of cetaceans: (*a*) *Eubalaena*; (*b*) *Sibbaldus*; (*c*) *Globiocephala*; and (*d*) *Platanista*.

Figure 2:   Skeletal anatomy of several cetacean species.

from Howell, 1930a
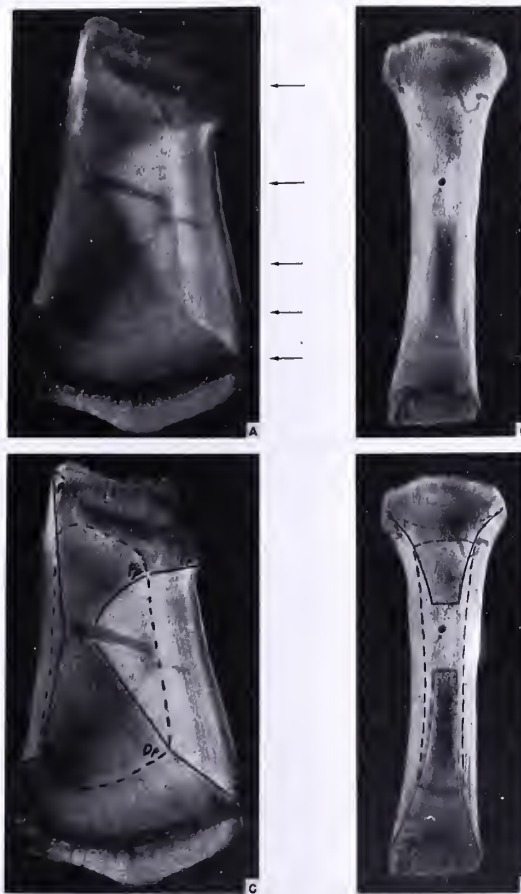
Fig. 8 Radiographs and interpretative line drawings of 5 mm thick anterior-posterior (at left) and medial-lateral longitudinal sections of radii of adult beluga. Both from same animal. M-1 section intersects a-p plane through apex of periosteal triangle posterior to point X. Relationships of periosteal and endochondral bone, as delimited at lower left and right, are described and discussed on p. 116. Abbreviations explained in text. Exposure at 500 MaS and 120 KV. × 3/5 natural size. (Arrows indicate levels of transverse sections shown in figure 9.)

Figure 3: Endochondral cones and neonatal outline within an adult beluga whale radius.

from Felts and Spurell, 1966

Yale University School of Medicine
Growth and Development Study Unit
Cetacean Flipper Development Study
Radiologic Survey

specimen log #   animal length

specimen tag #   animal weight

    species   flipper length

      sex

	1° centers	2° centers absent	appearing	developing	physes open	joined	closed	fused
Humerus								
Radius								
Ulna								
Carpals								
Metacarpals I								
II								
III								
IV								
V								
Digits I								
II								
III								
IV								
V								

Remarks:

Figure 4: Scoring sheet used in this study

Figure 5: Radiograph #500231F, a 142 cm male fetus.

   5A: Dorso-ventral view of flipper.

   5B: Detail view to show endochondral cones.
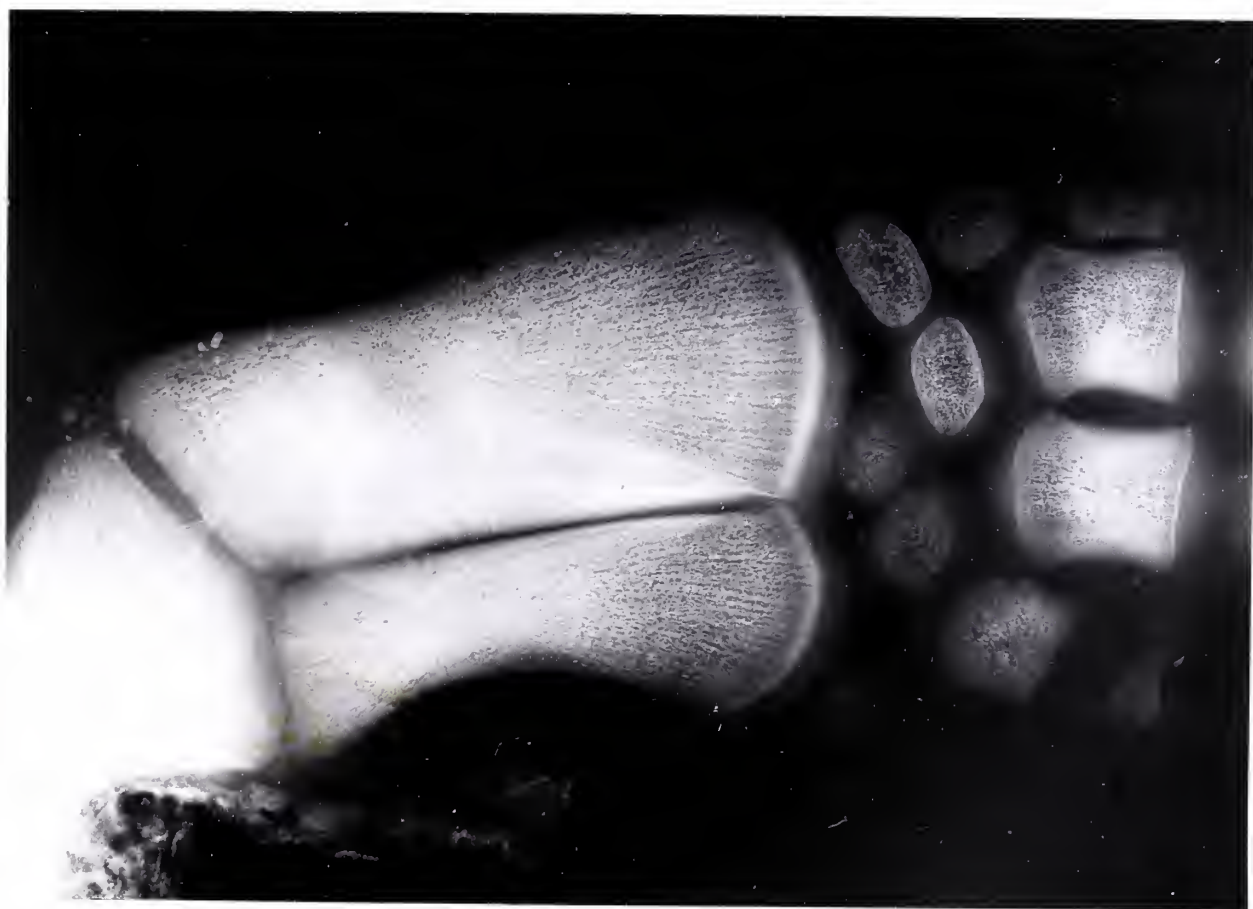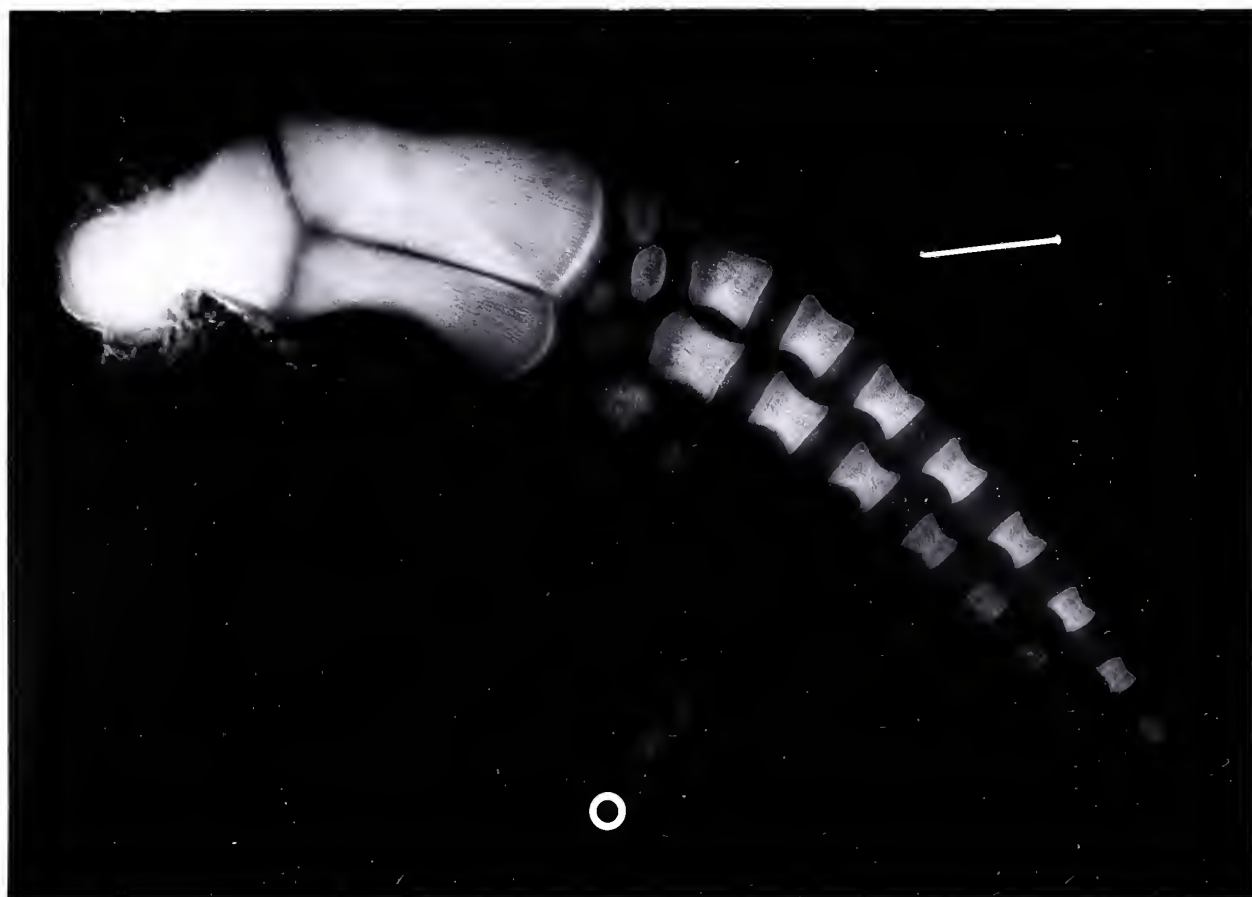
Figure 6:   Specimen C-186, a 37.0 cm flipper from a 223 cm, 180 kg male.

6A: Dorso-ventral radiograph

6B: D-V view to show   6C: Antero-postero
      epiphyses at elbow   view of proximal
                                     humerus. Note
                                     multiple ossifi-
                                     cation centers.

6D: Sectioned flipper

YALE GR DEV

YALE GR DEV

C-186/F

METRIC 1 2 3 4 5

C-186
F
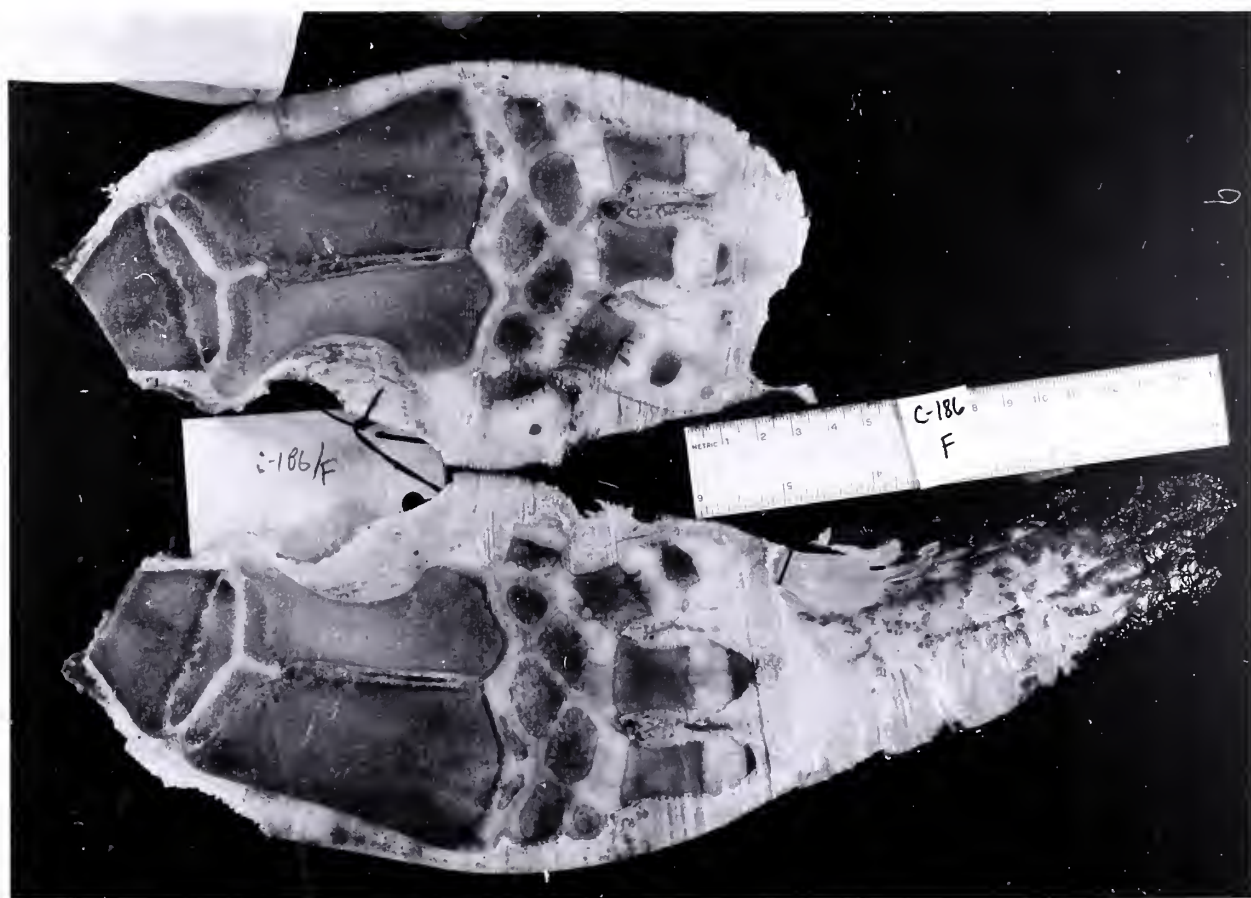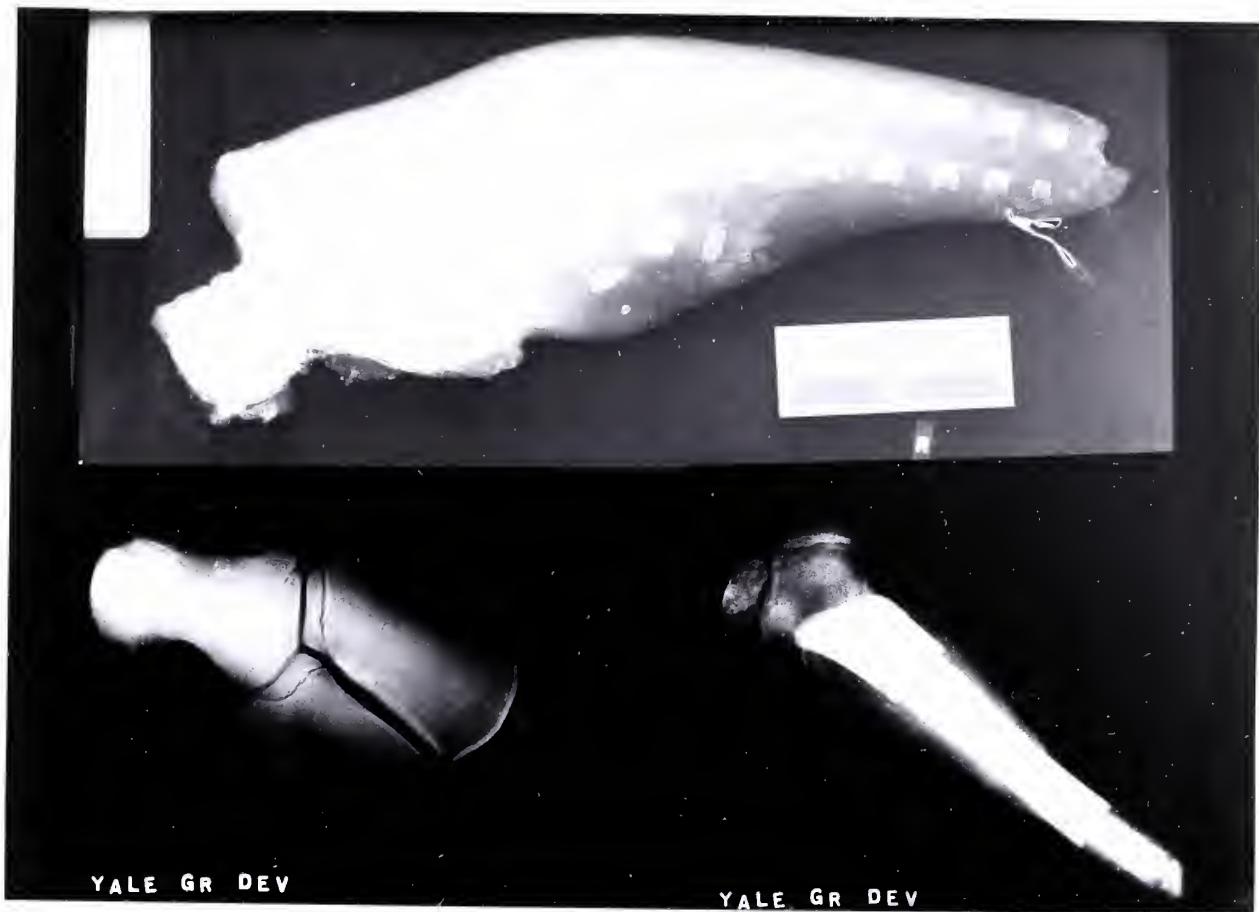
Figure 6, cont.

6E: Sectioned humeral head; humeral tubercle in center of photograph, articular surfaces at the sides of the photograph.

C-186
F
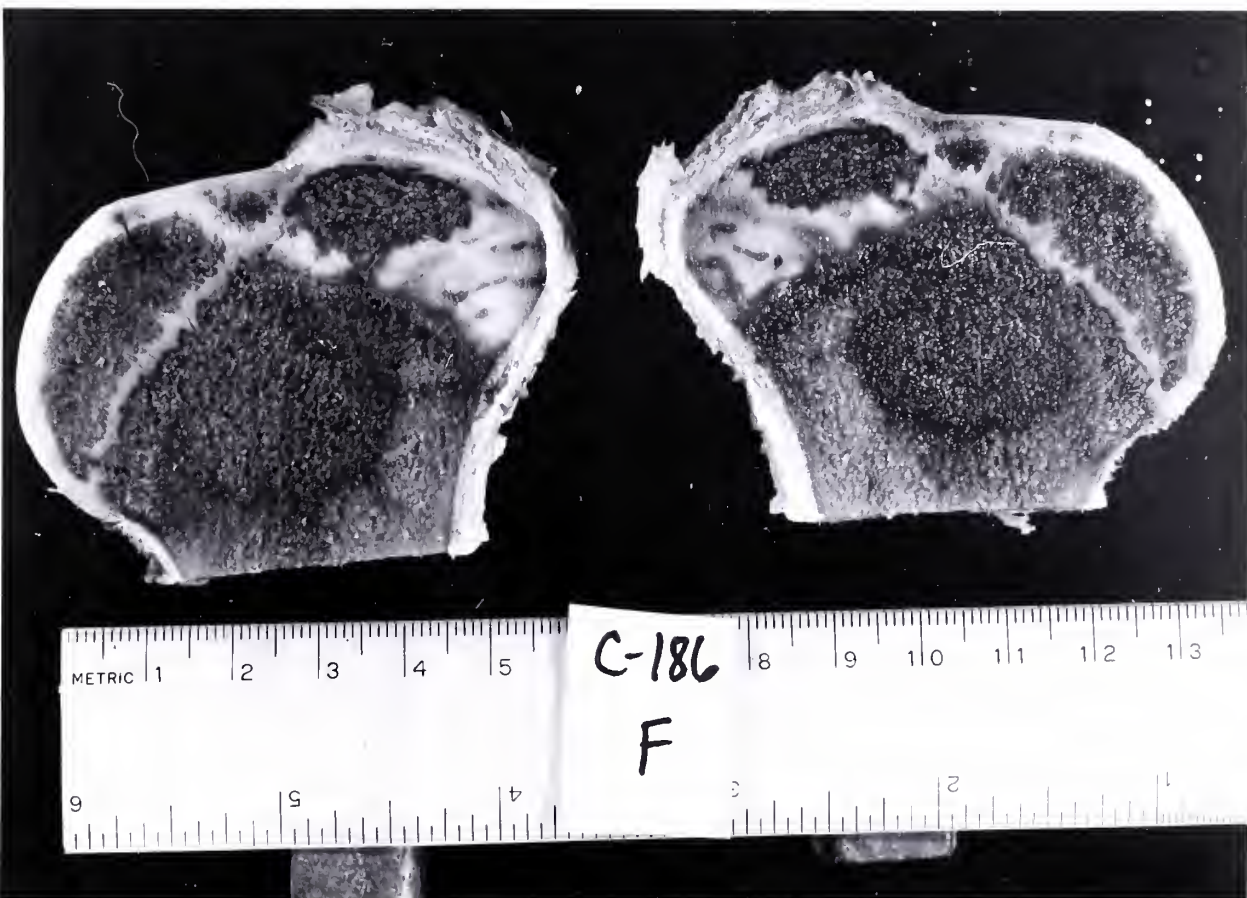
Figure 7: Specimen C-104, a 42.5 cm flipper from a 262 cm male.

7A: Dorsal-ventral radiograph

7B: Sectioned flipper

C-104
7
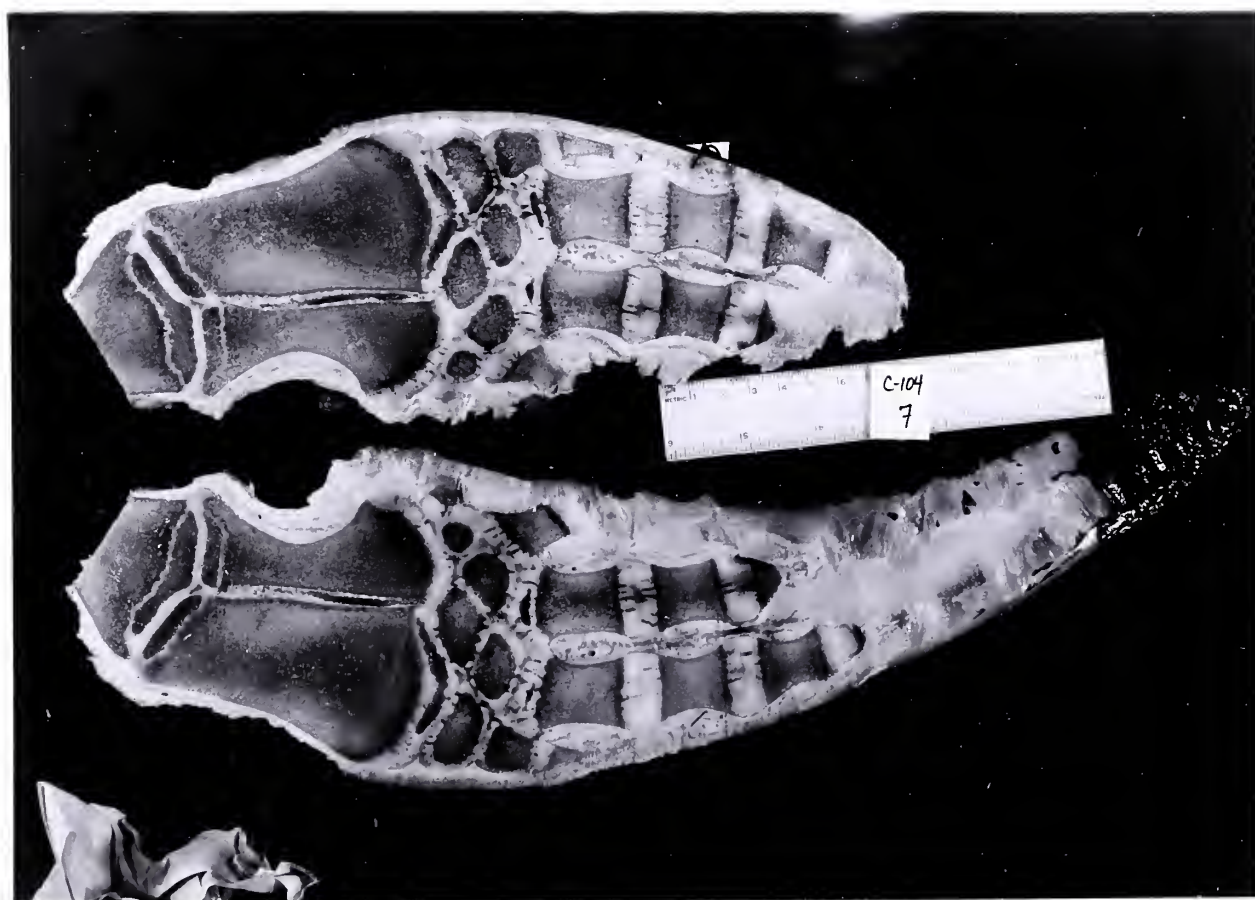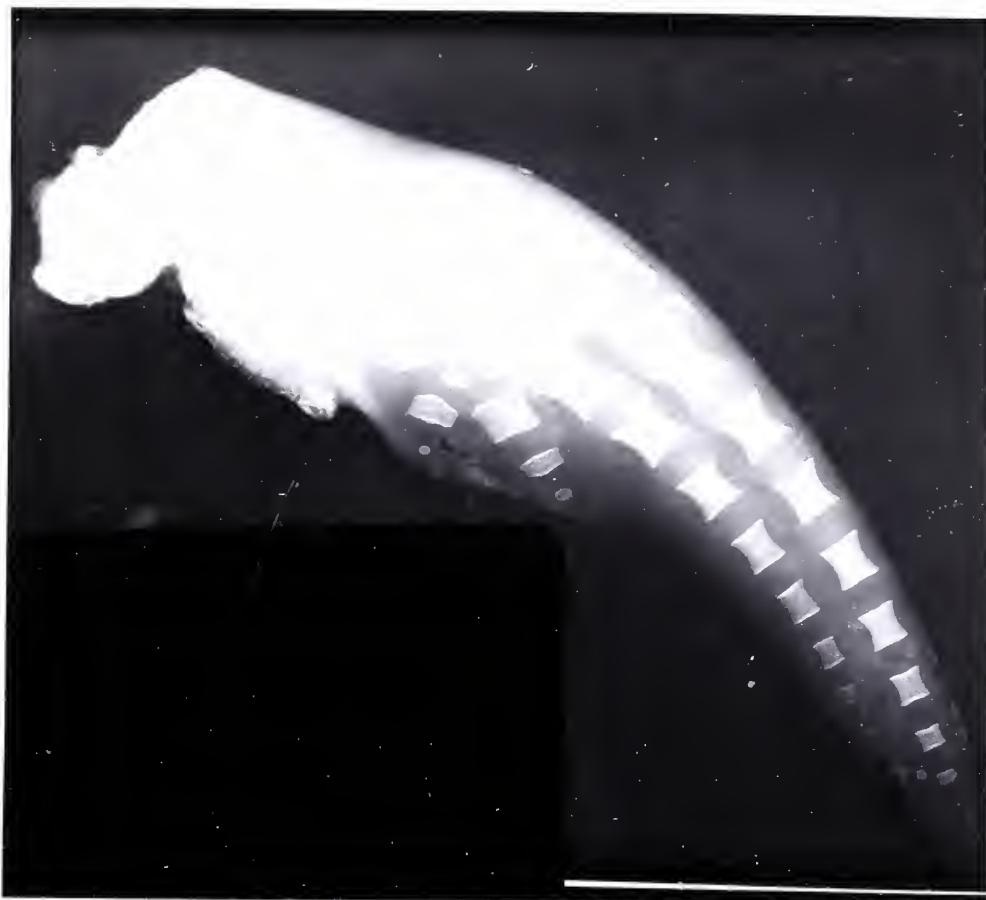
Figure 7, cont.

7C: Sectioned humeral head

C-104

7

Figure 8: Specimen C-107, a 44.5 cm flipper from a 265 cm female

8A: Dorsal-ventral radiograph

8B: Sectioned flipper

YALE GR DEV

11

C-107
11

Figure 8, cont.

8C: Sectioned humeral head

C-107
11

Figure 9: Specimen C-161, a 50.5 cm flipper from a 301 cm female

9A: Dorsal-ventral radiograph

9B: Sectioned flipper

YALE GR DEV

C-161
III
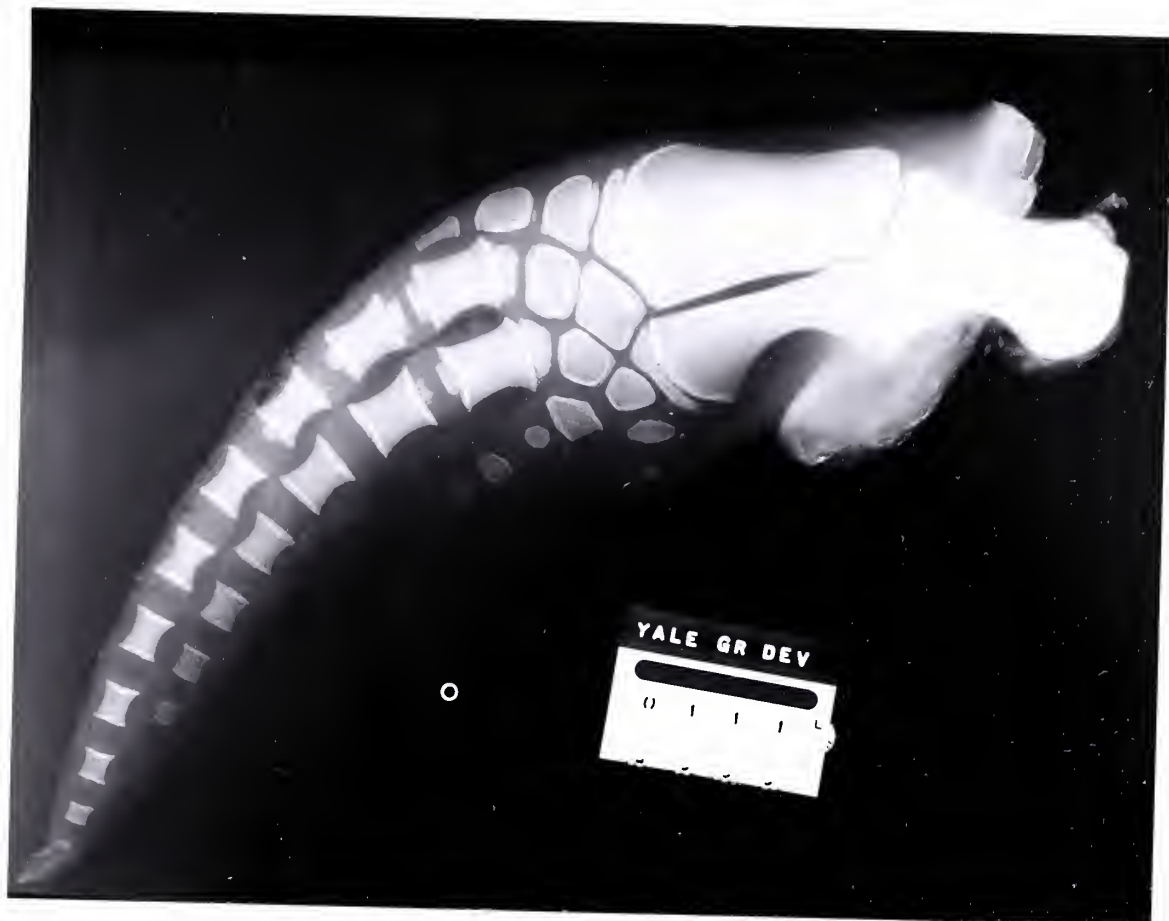
Figure 9, cont.

9C: Detail radiograph of carpus

9D: Detail photograph of sectioned carpus

C-161
111
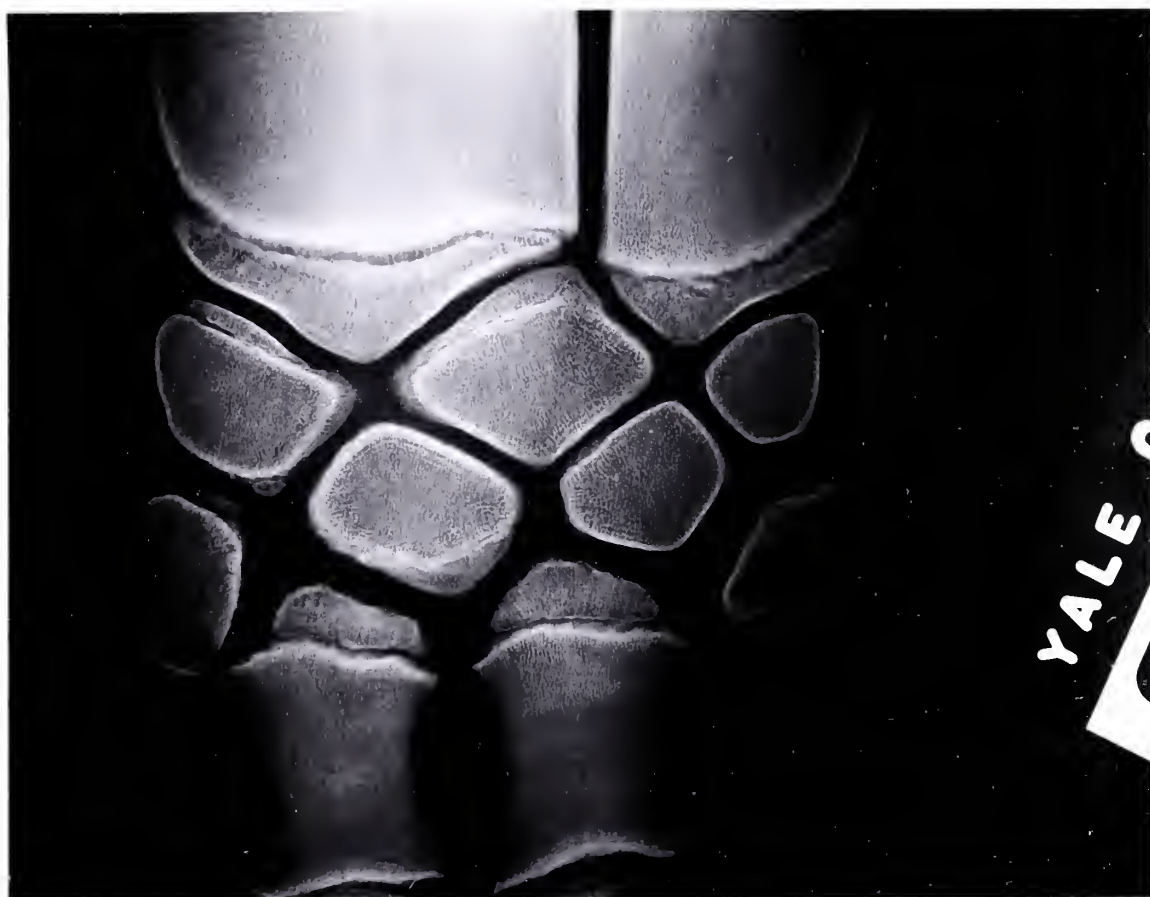
Figure 9, cont.

9E: Sectioned humeral head

C-161
III
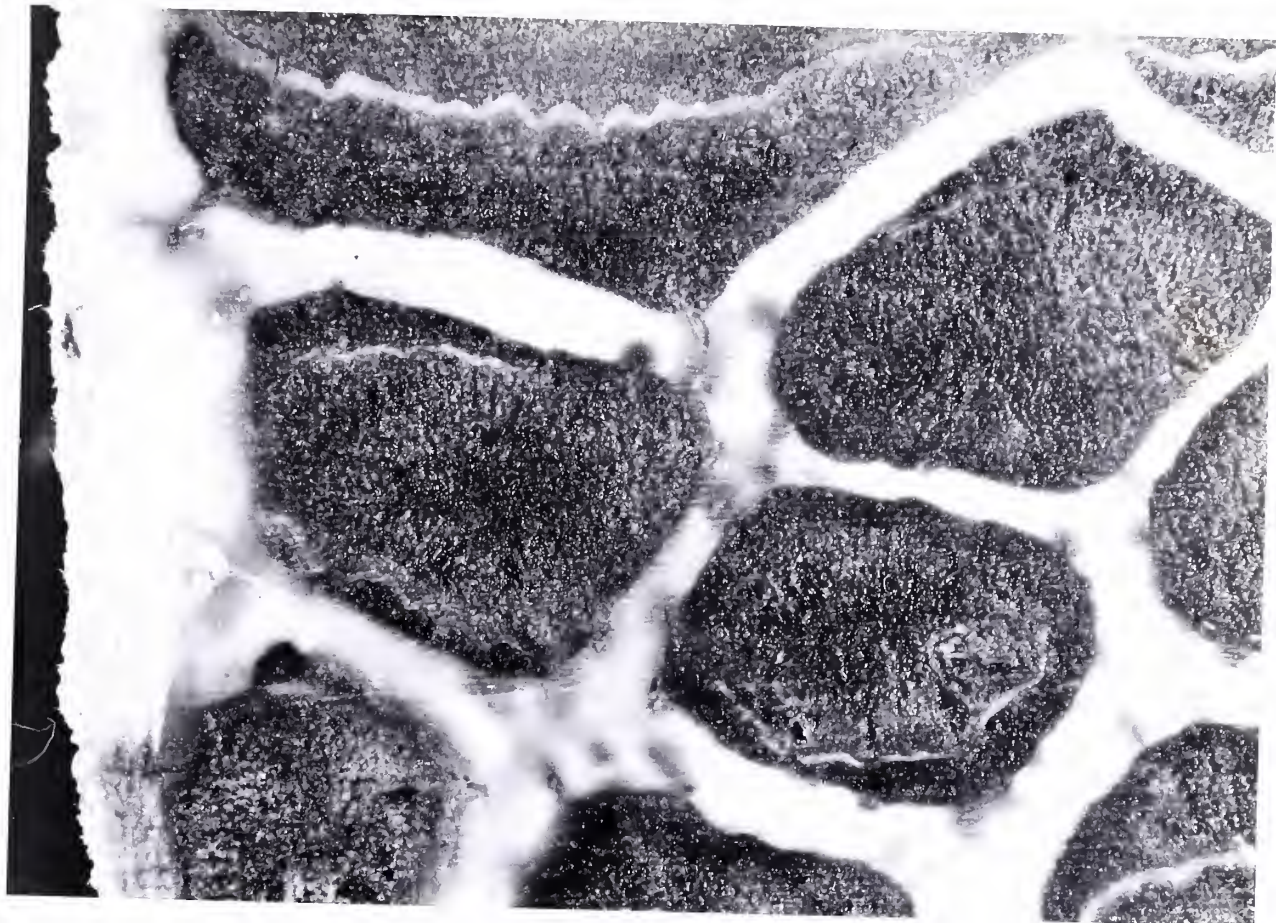
Figure 10: Specimen C-184, a 58.5 cm flipper from a
            327 cm, 360 kg female

    10A: Dorsal-ventral radiograph

    10B: Sectioned flipper

YALE GR DEV
D

O   L

C-184
D
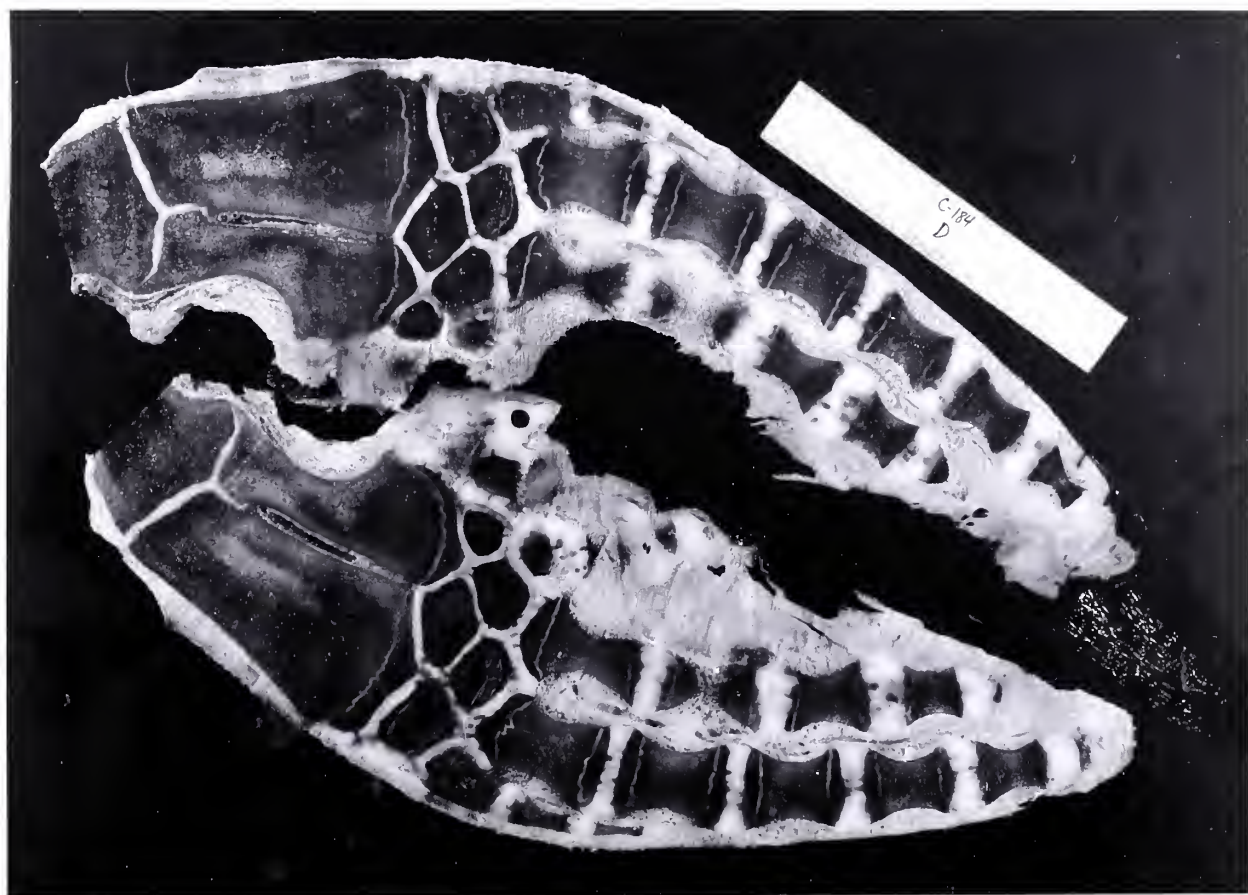
Figure 10, cont.

10C: Detail radiograph of carpus

10D: Detail photograph of sectioned carpus

C-184
D
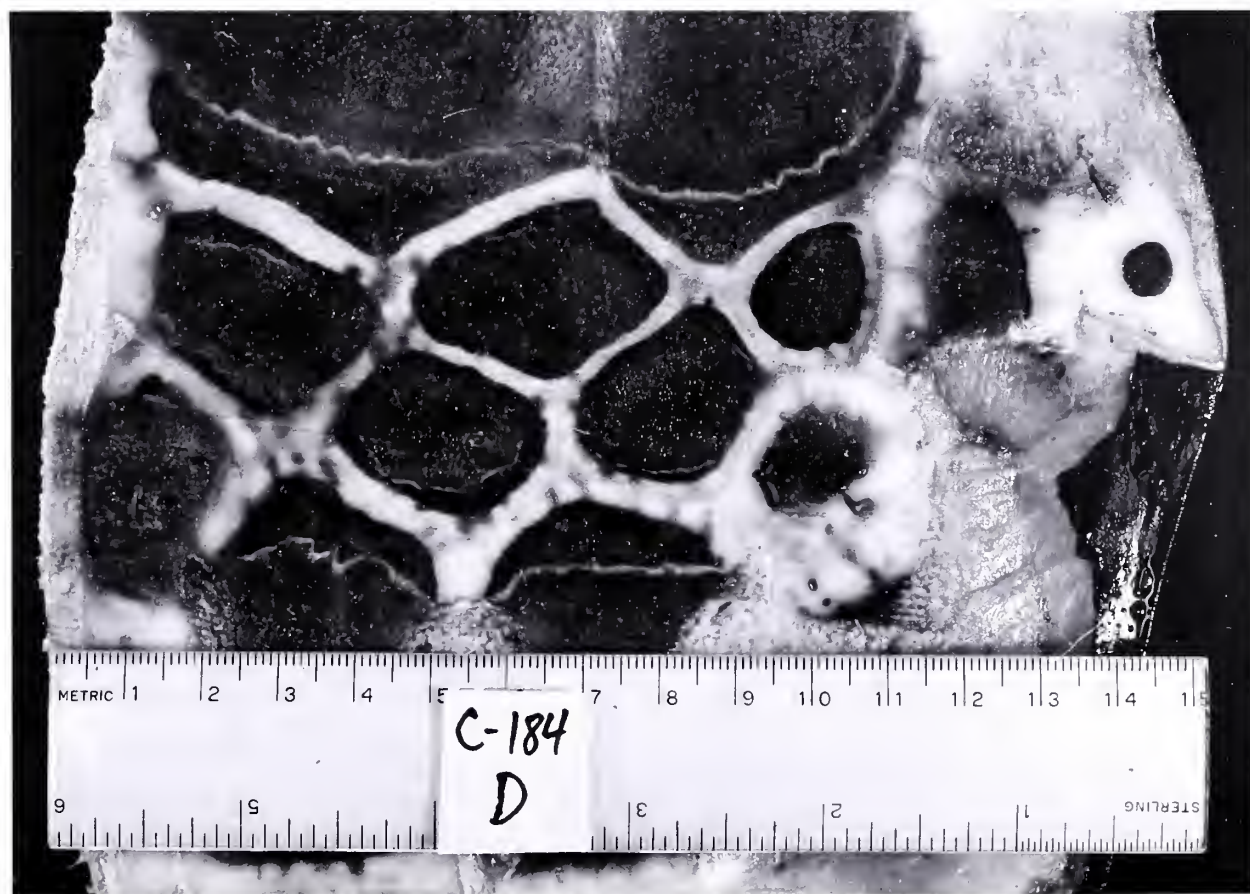
Figure 10, cont.

10E: Detail view of radial carpal, intermediate
      carpal, a portion of C1, and C2

10F: Sectioned humeral head

C-184
D

Figure 11: Specimen C-150, a 59.0 cm flipper from a
            360 cm, 620 kg female

    11A: Dorsal-ventral radiograph

    11B: Sectioned flipper

C-150
94
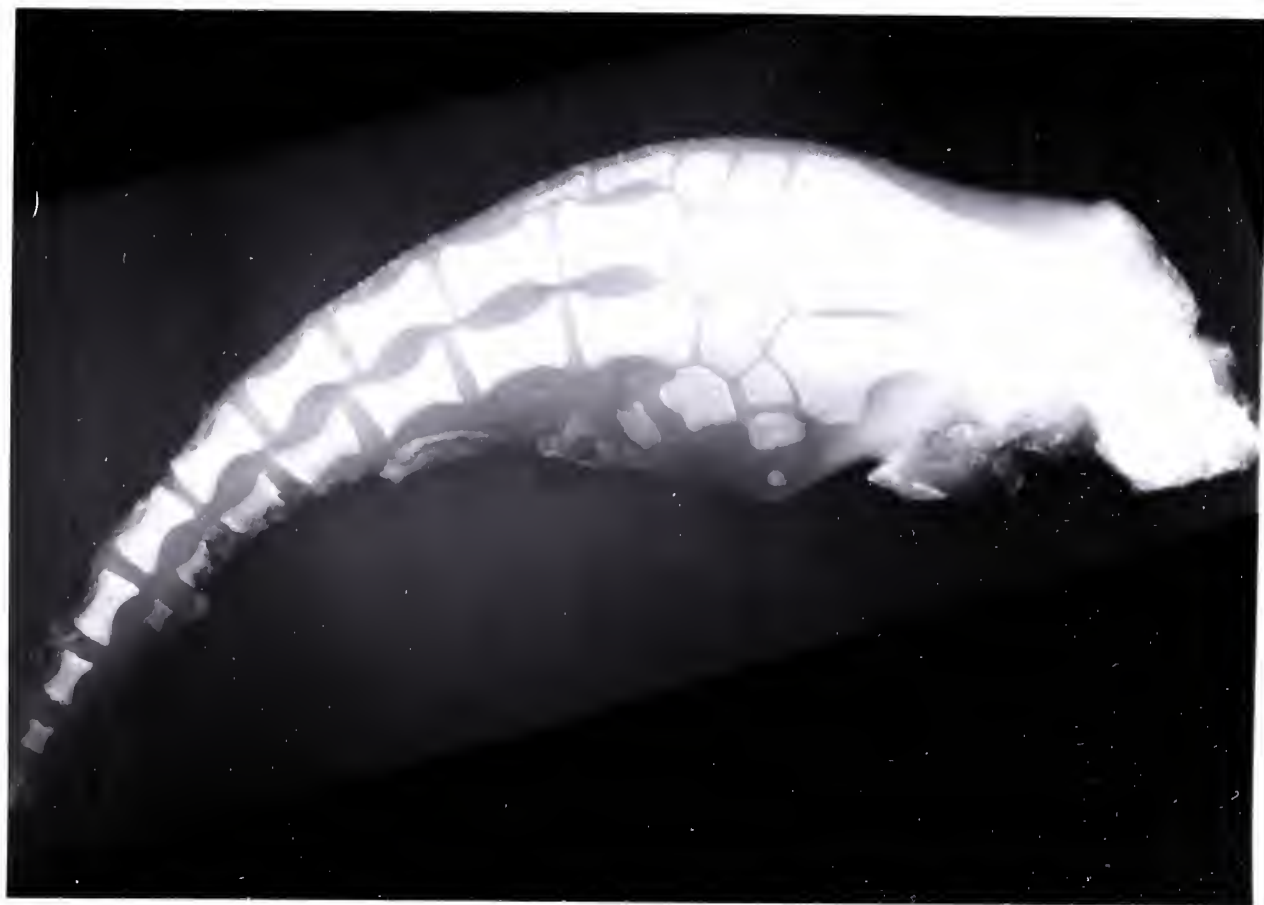
Figure 11, cont.

11C: Detail D-V view to show the ankylosis of the
humeral-ulnar joint

11D: Detail radiograph to show an accessory central
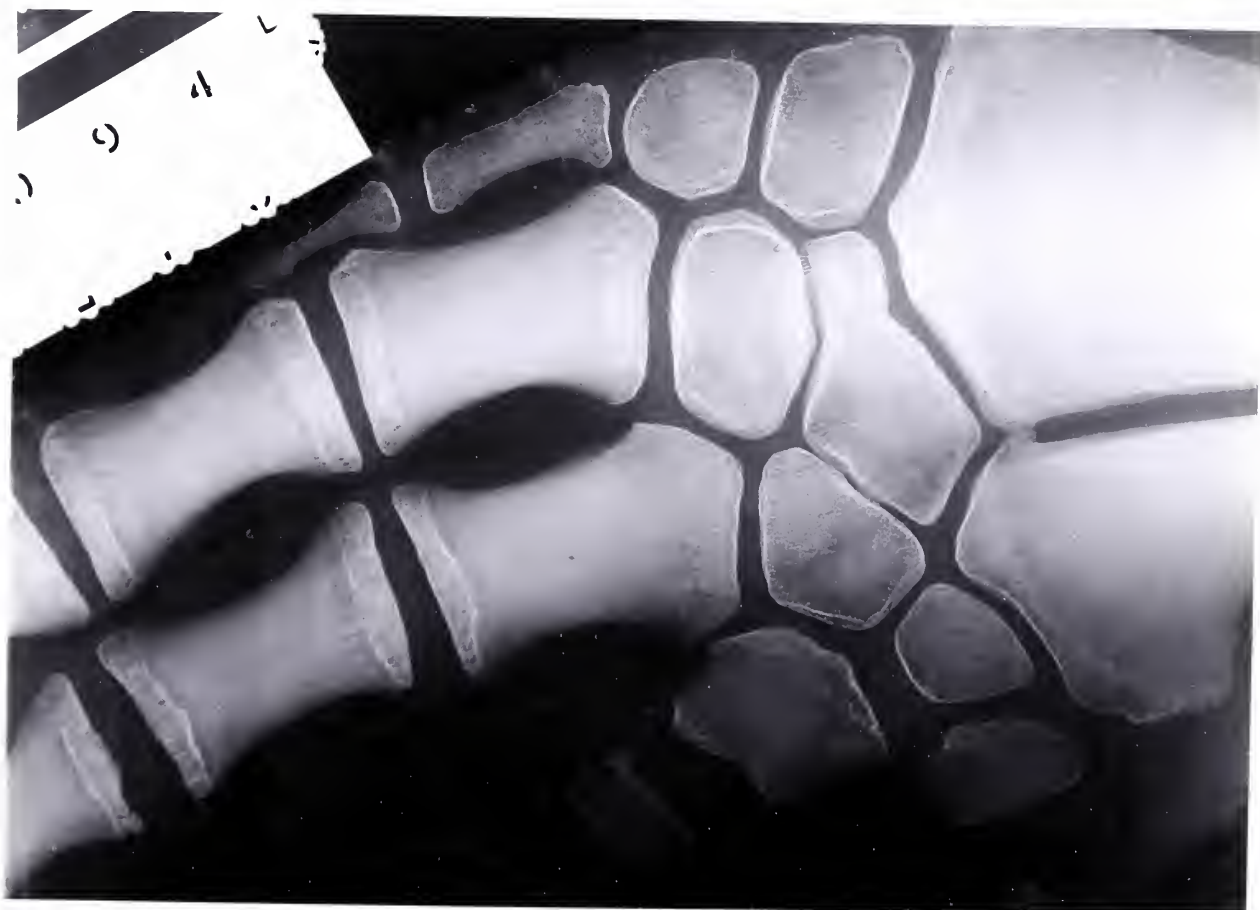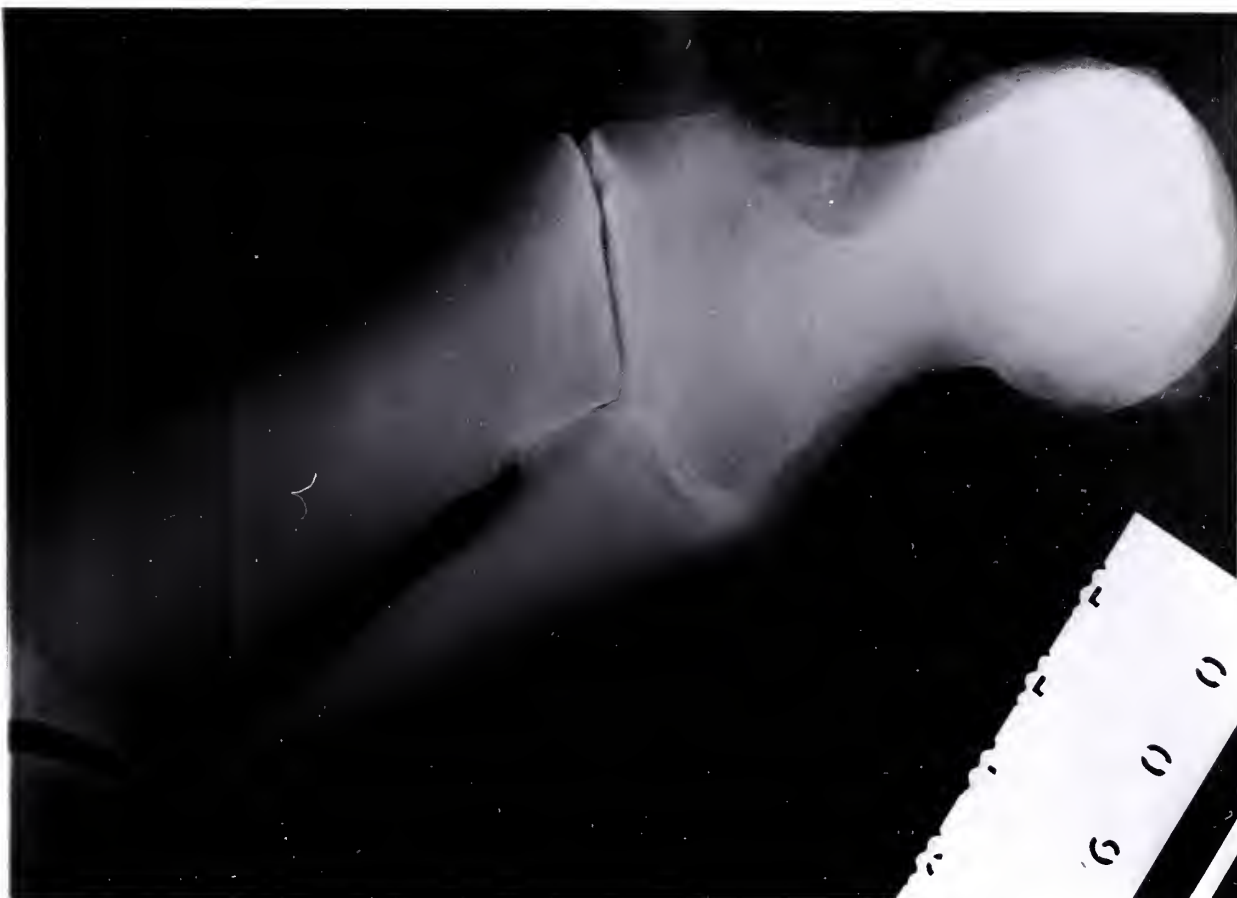carpal fused to the intermediate carpal

Figure 11, cont.

11E: Sectioned humeral head

METRIC 1 2 3 4 5 3 9 10 11 12 13 14 15

C-150
94

6 5 4 2 1

Figure 12: Radiograph of the terminal phalanges of specimen C-108, a 70.0 cm flipper from a 378 cm male

Figure 13: Radiograph 500225, a 70.0 cm flipper from a 358 cm male

13A: Radiograph of carpals, metacarpals, and
proximal phalanges

13B: Detail of radiograph showing the second and
third metacarpal-phalangeal joints, the
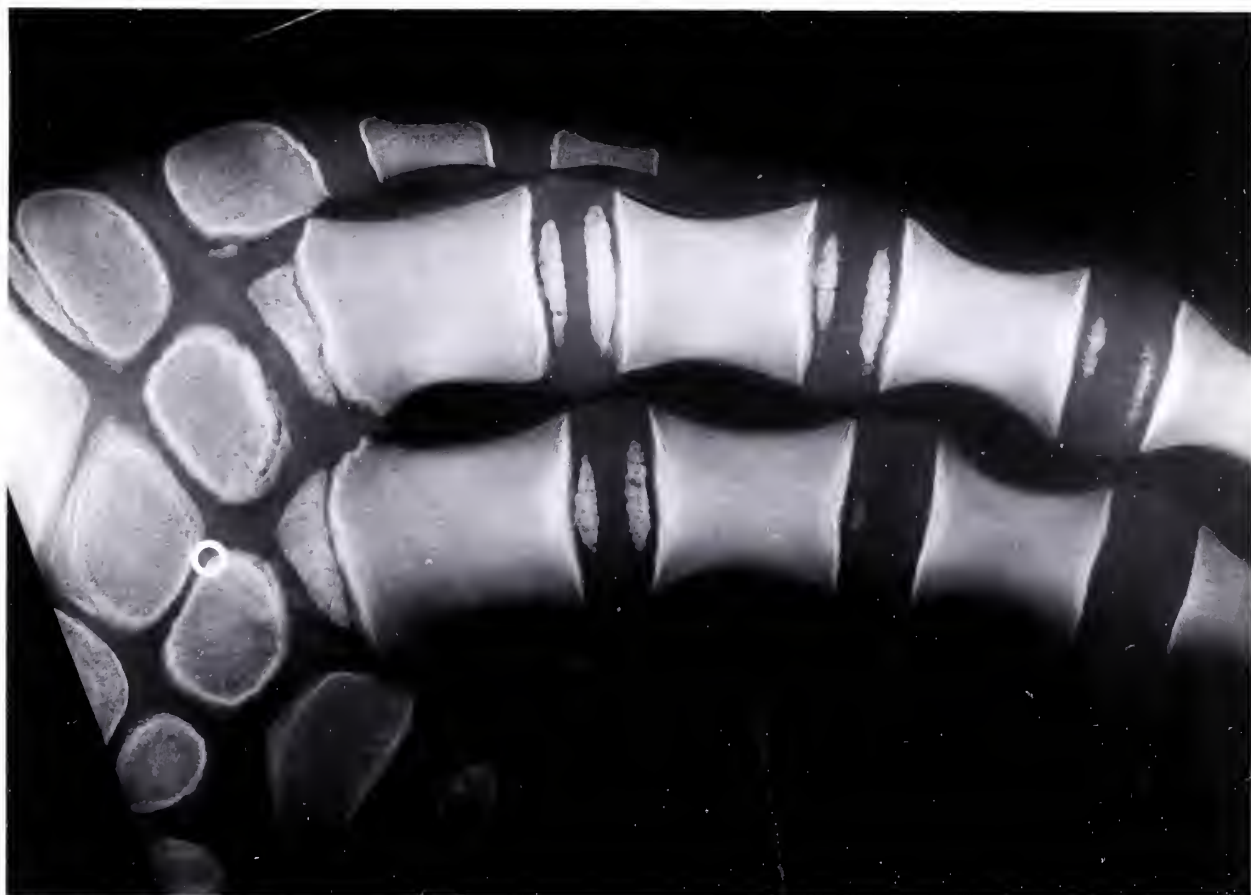digital epiphyses, and their transphyseal
cartilage canals

Figure 13, cont.

13C: Detail of radiograph showing the first interphalangeal
joints of the second and third digits, the digital
epiphyses, and the cartilage canals

Figure 14: Specimen C-90, a 66.0 cm flipper from a
375 cm, 720 kg female

14A: Bones of the flipper after cleaning by
Dermestid larvae. Several of the smaller
terminal phalanges were lost in processing.

14B: Close-up of the synostoses at the humeral-ulnar,
proximal radioulnar, and ulnar carpal-fifth
metacarpal joints.

C-90

a
s
d

n
h
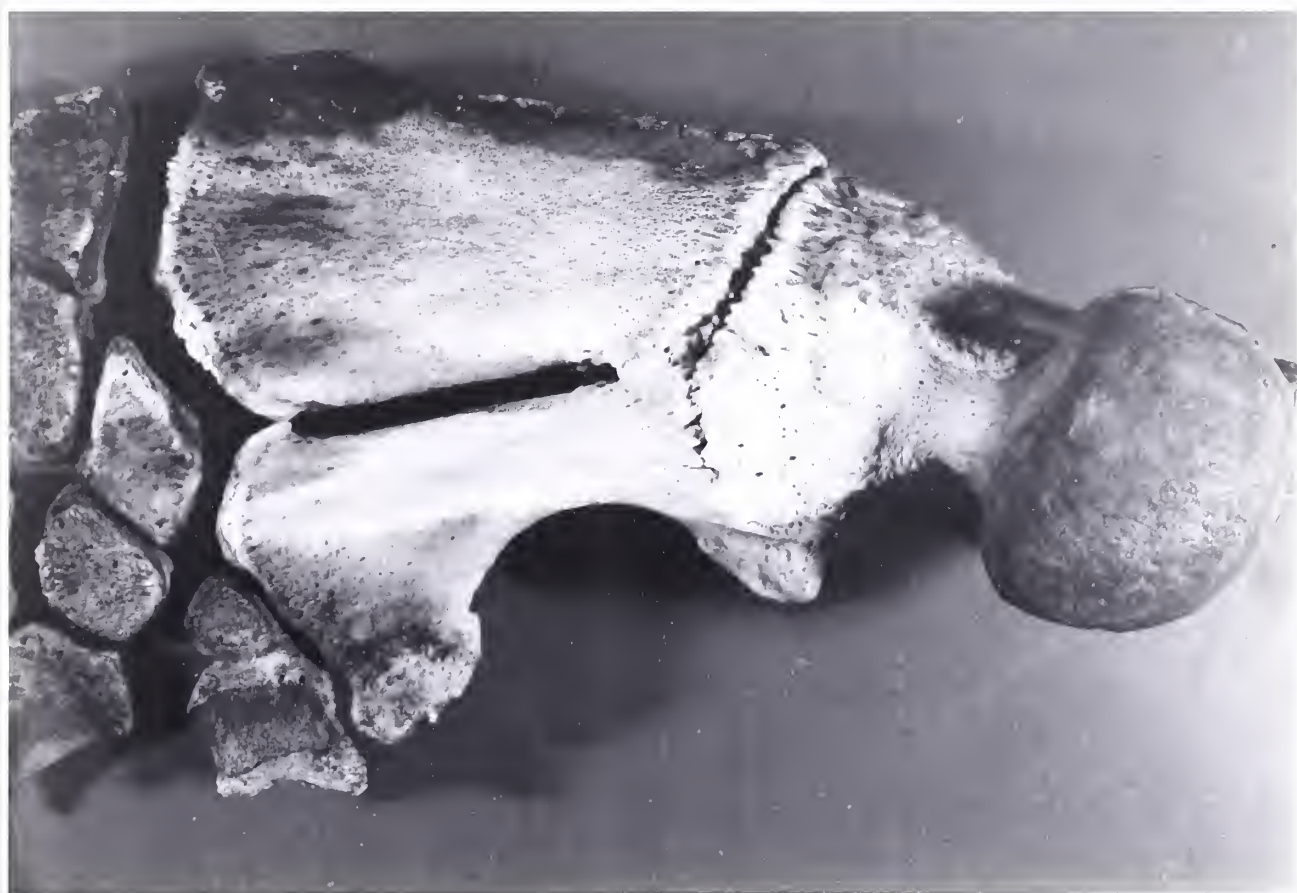
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